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Palaeoecological reconstruction of Late-glacial vegetation dynamics in eastern Baltic area: a view based on plant macrofossil analysis

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Declaration: Hereby I declare that this doctoral thesis, my original investigation and achievement, submitted for the doctoral degree at Tallinn University of Technology has not been submitted for any academic degree.

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Hilisjääaegsed taimkatte muutused Ida-Baltikumis taimsete makrojäänuste analüüsi põhjal

LEELI AMON

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LIST OF ORIGINAL PUBLICATIONS

I Amon L., Heinsalu A. and Veski S. 2010. Late glacial multiproxy evidence of vegetation development and environmental change at Solova, southeastern Estonia. Estonian Journal of Earth Sciences 59, 151–163.

II Amon L. and Saarse L. 2010. Postglacial palaeoenvironmental changes in the surroundings of Udriku, North Estonia. Geological Quarterly 54, 85–95.

III Amon L., Veski S., Heinsalu A. and Saarse L. Timing of Lateglacial vegetation dynamics and respective palaeoenvironmental conditions in southern Estonia: evidence from the sediment record of Lake Nakri. Journal of Quaternary Science (DOI: 10.1002/jqs.1530).

IV Veski S., **Amon L.**, Heinsalu A., Saarse L. and Vassiljev J. Late-Glacial vegetation dynamics in the eastern Baltic region, a complete record since the Bølling (GI-1e) (manuscript).

The author's contribution: planning of the project, organizing and contributing in fieldworks, plant macrofossil analysis, providing material for AMS radiocarbon datings (Papers I–IV), loss-on-ignition analysis (Paper I), data analysis, compilation of diagrams, interpretation of paleobotanical data, writing and contributing to the manuscripts (Papers I–IV).

Related publications not included in this thesis:

Kihno K., Saarse L. and **Amon L.** 2011. Late Glacial vegetation, sedimentation and ice recession chronology in the surroundings of Lake Prossa, central Estonia. Estonian Journal of Earth Sciences 60, 147–158.

Saarse L., Heinsalu A., Veski S., **Amon L.** and Gaidamavičius A. 2011. Deglaciation chronology of the Palivere ice marginal zone, northern Estonia (submitted to Bulletin of the Geological Society of Finland).

Saarse L., Niinemets E., **Amon L.**, Heinsalu A., Veski S. and Sohar K. 2009. Development of the late glacial Baltic basin and succession of the vegetation cover as revealed at Palaeolake Haljala, northern Estonia. Estonian Journal of Earth Sciences 58, 317–333.

ABBREVIATIONS

SIS – Scandinavian Ice Sheet
LG – Late-glacial
LGM – last glacial maximum
BP – before present (AD 1950)
cal y BP – calibrated years before present (AD 1950)
PAR – pollen accumulation rate
AR – accumulation rate
MS – magnetic susceptibility
LOI – loss-on-ignition

1. INTRODUCTION

The eastern Baltic area has been repeatedly glaciated and deglaciated during the Quaternary period. The last glacial–interglacial cycle sculpted the present topography of the study area and forced the restart of vegetation development after deglaciation. During the last glacial maximum (~20 000–22 000 cal y BP), the Scandinavian Ice Sheet merged (SIS) with the Kara Ice Sheet and the Barents Ice Sheet (Rinterknecht *et al.* 2006), forming a vast Eurasian Ice Sheet complex. The southeastern sector of the SIS extended over Scandinavia and the Baltic countries to northwestern Russia, Belarus, and Poland. The history of deglaciation, in particular the timing and pattern, of the eastern Baltic region is still under debate (Zelčs and Markots 2004, Kalm 2006, Kalm *et al.* 2011, Rinterknecht *et al.* 2006, 2008). The retreat of the SIS and the changing climate triggered major shifts in terrestrial vegetation ecosystems. Late-glacial (LG) vegetation succession was influenced by a combination of factors, including the Late Weichselian deglaciation pattern (Kalm 2006, Rinterknecht *et al.* 2006, Kalm *et al.* 2011), the regional migration rate of plants (Huntley and Birks 1983, McLachlan *et al.* 2005, Pearson 2006, Svenning *et al.* 2008), local plant succession, soil development (Egli *et al.* 2006), and climatic change.

The history of the eastern Baltic deglaciation has been studied for over a century (latest overviews in Zelčs and Markots 2004, Kalm *et al.* 2011). Although there are about 100 absolute age estimations obtained from the Estonian LG sediment sequences (Kalm 2006), only a few may be associated with biostratigraphical studies, therefore resulting in the lack of adequately dated biostratigraphical reference sites that might serve as the basis of chronologically precise palaeoenvironmental reconstructions. Consequently, almost all of the LG sequences in the eastern Baltic area are, in general, not independently dated, and they are solely described by the comparison of pollen zones and pollen percentage data without plant macrofossil studies (Thomson 1935, Pirrus 1969, 1971). Moreover, ^{14}C-dated investigations of LG vegetation succession in latitudinally adjacent areas do not exist, with the exception of some sites in eastern Karelia (Wohlfarth *et al.* 1999, 2004, 2007), Latvia (Heikkilä *et al.* 2009), and Lithuania (Stančikaitė *et al.* 2008, 2009). It has been demonstrated by a number of studies that pollen-based reconstructions in treeless landscapes need validation for plant macrofossil record (Birks and Birks 2000). Nevertheless, there are some plant macrofossil studies from Latvia (e.g., Heikkilä *et al.* 2009, Kalnina *et al.* 2011), and until this thesis, none in Estonia.

The aims of the present thesis are:

1. explore the LG vegetation development along a south–north (S–N) transect from distal to proximal areas of the ice margin of SIS;
2. reconstruct the dominant species/communities and estimate the age of migration of pioneering plant species into areas that were formerly covered by ice sheets;
3. compare the possible relationships between LG and modern arctic communties;
4. demonstrate the response of vegetation to oscillations in the climate during the LG period ca. 14 650–11 650 cal y BP;
5. discuss the first unambiguous palaeobotanical record of the LG Bølling (GI-1e) warming in the eastern Baltic area;
6. characterize the impact of the Older Dryas (GI-1d) cold spell;
7. define the pollen accumulation rates (PAR) of dominant LG tree and shrub taxa according to which macrofossil evidence is present;
8. discuss the newly acquired radiocarbon age estimations of the start of floral development with present knowledge on deglaciation history;
9. propose new estimations for the ice marginal zones.

2. DEGLACIATION OF THE SOUTHEASTERN FLANK OF THE SCANDINAVIAN ICE SHEET

2.1. Deglaciation pattern

Several glacial–interglacial cycles, driven by oscillations in orbital forcing, Earth's radiation balance, changes in greenhouse gases, and thermohaline circulation, have shaped the Earth's surface during the Quaternary period (Solomon *et al.* 2007). Traces of different Quaternary glaciations have been recorded in various parts of Europe (Svendsen *et al.* 2004, Ehlers and Gibbard 2004, Ehlers *et al.* 2011). Growth of the last major ice sheets in the world to their maximum positions in response to climate forcing (decreases in northern summer insolation, tropical oceanic surface temperatures, and atmospheric CO_2) occurred between 33 000 and 26 500 cal y BP (Clark *et al.* 2009). The ice sheets reached their maximum extent, i.e., last glacial maximum (LGM), shortly after 26 500–20 000/19 000 cal y BP (Clark *et al.* 2009). The last glaciation event that also affected the northern part of Europe, the Late Weichselian glaciation, started around 28 000 cal y BP and reached its culmination about 22 000–18 000 cal y BP (Ehlers *et al.* 2007).

The SIS that influenced Northern Europe, including the Baltic area, was active during the Weichselian glaciation. As the SIS was far more extensive during the Late Weichselian glaciation (Ehlers *et al.* 2007), the earlier ice margin positions and glacial sediments are underrepresented due to overprint by younger deposits (Lambeck *et al.* 2010). In its maximum position, the SIS merged with the Barents Ice Sheet and the Kara Ice Sheet forming the Eurasian Ice Sheet complex (Rinterknecht *et al.* 2006).

The exact position of the LGM limit in the Baltic area is still under debate (Raukas 2009) and numerous versions have been published (Kalm 2010 and references therein). Also, the correlation of both the LGM and deglaciation in areas affected by the SIS might be difficult – at some locations the ice retreated but in another place at the same period it advanced (Lambeck *et al.* 2010); ice retreats and advances were not synchronous over the area.

The SIS began to retreat after LGM between 20 000 and 19 000 cal y BP (Clark *et al.* 2009). The deglaciation was a complicated process, induced both by climatological and geological factors. Most authors hold with the idea of deglaciation stadials and interstadials (oscillations), i.e., cold periods when ice advances and warm periods when ice retreats (Raukas 2009, Zelčs and Markots 2004). The glaciodynamic deglaciation paradigm has been questioned and the idea of spatially asynchronous deglaciation of the SIS with surface thinning across a large area has been proposed (Bitinas 2011).

Table 1. Correlation of ice marginal zones in eastern Baltic area. EE – Estonia; LV – Latvia.

Ice marginal zone	Regional correlation	Age estimation, reference
Palivere	Palivere (EE)	12800–12700 cal y BP (Kalm 2006); 12700 cal y BP (Kalm *et al*. 2011); 13200 cal y BP (Saarse *et al*. subm.)
Pandivere	Pandivere (EE)	13800 cal y BP (Saarse *et al*. 2009); 13300 cal y BP (Saarnisto and Saarinen 2001)
Otepää	Otepää (EE)	14700–14500 cal y BP (Kalm 2006); >14000 cal y BP (Kalm *et al*. 2011)
	Haanja (EE)	15700–14700 cal y BP (Kalm 2006; Kalm *et al*. 2011)
North Lithuanian	Linkuva (LV)	15600–15400 cal y BP (Kalm 2006); ~13200 ^{14}C y BP (Zelčs and Markots 2004) (median ~16100 cal y BP)
	North Lithuanian (LV)	13300±700 ^{10}Be y BP, 13300±1100 ^{14}C y BP (Rinterknecht *et al*. 2008) (median ~16000 cal y BP)
Middle Lithuanian	Gulbene (LV)	13500±600 ^{10}Be y BP, 13500±1000 ^{14}C y BP (Rinterknecht *et al*. 2008) (median ~16300 cal y BP)

Classically, deglaciation is described with ice marginal formations (e.g., Rinterknecht *et al*. 2006) (Table 1). The deglaciation of Latvia is divided into different stages: Dagda, Gulbene, Linkuva, and Valdemarpils (Zelčs and Markots 2004). In the first stage, a complex lobate structure with many small glacier tongues existed. Later, the ice pattern and dynamics simplified and only the largest ice lobes remained active in the lowlands (Zelčs and Markots 2004). In Estonia, four (Haanja, Otepää, Pandivere, and Palivere) (Kalm 2006) or five (Haanja, Otepää, Sakala, Pandivere, and Palivere) (Pirrus and Raukas 1996) ice marginal zones have been differentiated. It has been suggested that the hilly topography of South Estonia was formed mainly due to the effect of stagnant ice, whereas that of North Estonia was shaped by active ice (Raukas 2009). The correlation of these landforms may be complicated as they are usually fragmented several tens of kilometers long and difficult to trace to other regions (Bitinas 2011). However, attempts for the correlation and application of different dating means have been carried out (Rinterknecht *et al*. 2006).

Despite a long research history of Baltic deglaciation, several issues have remained unclear. Raukas (2009) confessed the insufficiency of the present chronological scheme of deglaciation on the Estonian territory and the problems with dating methods, especially the optically stimulated luminescence (OSL) datings of LG minerogenic sediments (Raukas *et al*. 2010). Although there are about 100 absolute age estimations from the Estonian LG sediment sequences (Kalm 2006), only a few may be associated with biostratigraphical studies. Consequently, almost all of the LG sequences in Estonia and the eastern Baltic area are, in general, not independently dated, and they are solely described by the comparison of pollen zones and pollen percentage data. The LG-stratigraphical subdivision of Estonia comprises two stadials (Older Dryas and Younger Dryas) and one interstadial (Allerød), which are distinguished mainly on the basis of palynological data (Pirrus 1976, Pirrus and Raukas 1996). Their chronostratigraphical positions have been established by a few radiocarbon dates, thermoluminescence, OSL, and ^{10}Be dating of the tills, and other glacigenic deposits and erratic boulders (Kalm 2006, Rinterknecht *et al.* 2006, Sohar and Kalm 2008, Raukas *et al.* 2010).

2.2. Late-glacial chronology

Since Iversen (1942, 1953), the classic biostratigraphical and chronostratigraphical setting of Europe has been established, modified by Mangerud *et al.* (1974) in terms of time transgressiveness and by Björck *et al.* (1998) in terms of linking the climatic events to episodes registered in the North Greenland ice core records. LG studies in the eastern Baltic area span over a century focusing on ice recession lines (Hausen 1913, Ramsay 1929) and chronology (Serebrjannyi and Raukas 1966). In recent years, the new data on ice retreat involve varvochronology (Sandgren *et al.* 1997, Hang 2003), new dating methods (Rinterknecht *et al.* 2006, 2008), and reviews (Raukas *et al.* 2004, Kalm 2005, 2006, 2010).

The LG period is characterized by remarkable climatic oscillations and therefore quickly changing environmental conditions. The chronology of key climatic events during LG is based on correlation of the ice-core, marine, and terrestrial records (Lowe *et al.* 2008). In literature, specific climatostratigraphical interval names are often used, e.g., Bølling, Allerød, and Younger Dryas. However, the nature of these units is time-transgressive and depends on the location, proximity to ice, etc. The climatic events scheme developed by Lowe and co-authors (2008) offers the possibility of comparing regions that are in different vegetation development stages by standardized units.

GS-1 (~11 650–12 850 cal y BP) / Younger Dryas
GI-1a (~12 850–13 050 cal y BP) / Allerød
GI-1b (~13 050–13 250 cal y BP) / Gertsenzee oscillation
GI-1c (~13 250–13 900 cal y BP) / Allerød
GI-1d (~13 900–14 050 cal y BP) / Older Dryas
GI-1e (~14 050–14 650 cal y BP) / Bølling

3. LOCAL VEGETATION IN DEGLACIATED AREAS

3.1. Pioneer plant communities in glacier forelands

There are no exact modern analogs to the LG communities as they developed in unique and changing environmental conditions (Birks 2003). Modern conditions and plant communities most similar to the LG ones are probably the newly deglaciated areas in polar or mountainous areas (Birks and Seppä 2010). Newly exposed moraines consist of a large part of coarse particles and very little or none of the biological legacy: organic matter content, propagules, etc. The first colonizers to establish glacier forelands, cyanobacteria, stabilized the soil and raised nutrient content (Hodkinson *et al.* 2003). The initial stage of the primary succession in deglaciated areas is characterized by the sporadic appearance of plant specimen and individuals. Plant communities in recently deglaciated areas are simple, and the species diversity is relatively low (Hodkinson *et al.* 2003). Subsequently, plant abundance increases, leading to population development and, consequently, to a more structured community (Mori *et al.* 2008). The pioneer communities are most affected by stochastic factors, e.g., seed dispersal, while later in succession, the deterministic factors (soil properties, length of vegetation period, etc.) will limit the species richness and diversity (del Moral 2009). Vegetation succession in newly deglaciated arctic areas is highly affected by low temperatures, short growing season, limited moisture and nutrient availability, and cryoturbation of soils (Hodkinson *et al.* 2003).

The observation of the development of pioneer vegetation in modern glacier foreland indicates that colonization is rather fast – the first plants will colonize newly exposed surfaces within few years or decades after the glacier retreat (e.g., Jones and Henry 2003). In harder climatic conditions, vegetation cover can reach 100% not earlier than 100 years after the deglaciation and the vegetation is still prostrate (Hodkinson *et al.* 2003). In the arid and nutrient-poor glacier foreland with long lasting snow cover, vascular vegetation cover has been under two percent for more than 200 years after deglaciation (pers. obs. in Svartdalen, Svalbard).

The plant species are divided into groups as early-, middle-, and late-successional species. Early colonizers may be able to use the bare substrate, but the later entries require facilitation (Hodkinson *et al.* 2003). In Norway, *Saxifraga cespitosa* occurred in less than seven years after deglaciation (Whittaker 1993) while *Saxifraga oppositifolia* and *Salix polaris* grew on the grounds deglaciated for two years (Hodkinson *et al.* 2003). The increase in the number of plant species migrating to the deglaciated area is highly affected by the input of adjacent communities (species pool). In alpine glacier forelands, where the possible migration source area is relatively close, pioneering plants (*Epilobium*, *Linaria*, *Saxifraga aizoides*, and different ferns and mosses) occur 5–7 years after the ice decay, and they grow less than 100 m from the glacier limit. About a decade from deglaciation, the first woody pioneer species were able to colonize the area, but usually as scattered individuals (Burga 1999). The development from tundra to forest consists of the following sequence: tundra → tundra with patches of forest → forest with patches of tundra → closed forest. The modern transition zone from the tundra biome to the boreal forest taiga is relatively narrow (30–150 km) although it covers 13 400 km^2 of the lands of the Northern Hemisphere (Callaghan *et al.* 2004).

Modern Arctic tundra is defined as low-growing vegetation beyond the cold limit of tree growth at high latitude (Walker *et al.* 2005). The present tundra communities are divided into subzones based on environmental conditions (mire tundra, snowbeds, etc.) (e.g., Elvebakk 1994), or at a larger scale, using bioclimatic zonation (Walker *et al.* 2005).

3.2. Plant macrofossil analysis – key to past local vegetation

The objective of palaeoecology is to study and reconstruct the ecology and dynamics of past communities; that of palaeobotany focuses on past vegetation. Different methods provide the basis for palaeobotanical approaches; most widespread and well known of them are pollen analysis and plant macrofossil analysis. Plant macrofossils are the plant remains or plant subfossil material that are visible to the naked eye and can be manipulated by hand (Birks 2001). It comprises not only different plant materials such as seeds, fruits, and spores, but also vegetative parts such as leaves, needles, and bark. The size of plant macrofossils varies from less than a millimeter to megafossils, e.g., tree trunks. Also, the remains of cryptogams and charophyte oospores are considered as parts of plant macrofossils analysis. Frequently, limnic animal remains are counted or identified during plant macrofossil analysis.

The plant macrofossil analysis was the main method for studying the floristic and vegetation history before the establishment of micropalentology, e.g., pollen analysis in the first part of 20th century. The popularity of pollen analysis led to the decline of the usage of plant macrofossil analysis, but soon, it was realized that these two methods complement each other and, in fact, should be used together. Plant macrofossil records have several qualities that pollen data lack (Birks 2008, Birks and Birks 2000):
1) Plant macrofossils can be identified for a higher taxonomic level, often to a species level.
2) There are plants that do not produce much pollen, are not wind-pollinated, or their pollen does not preserve well in sediments though they can be recovered by macrofossil analysis. For example, *Populus* pollen is more susceptible to corrosion than other pollen types (Campbell 1999) but *Populus tremula* catkin scales are often found in sediments and are rather easy to recognize.

3) Plant macroremains reflect mainly the local scale vegetation, i.e., the vegetation just around a lake or that growing on a bog, while pollen analysis represents the vegetation signal on a regional scale.
4) In the case of long-distance-transported or insensitive pollen data, plant macrofossils are a means of a realistic reconstruction and confirmation of the plant's actual presence. Many abundantly produced pollen grains are wind-dispersed and tend to dominate in the pollen spectra and pollen diagrams, especially during LG. Relying only on pollen would then lead to misinterpretation of past vegetation (Birks 2008).

The results of plant macrofossil analysis are usually the basis for local vegetation reconstructions. However, the interrelation between plant macrofossil assemblage and past vegetation is not straightforward (Differbacher-Krall 2007 and references therein). A certain plant macrofossil finding confirms the plant species' palaeo-presence in the studied sediment layer; however, the absence of a plant macrofossil cannot rule out the actual occurrence of that specific species. According to studies, plant macrofossil assemblage reflects about 40% (Davidson *et al.* 2005), 50% (Koff and Vandel 2008), or in mire sites, even 100% (Greatrex 1983) of the surrounding vegetation. Although the plant macrofossil data underestimates the species richness, it can still reflect dominant components of the vegetation (Zhao *et al.* 2006). The dispersion range of aquatic plant macrofossils from the actual plant in recent reference studies from shallow lakes is 15 to 100 m (20–30 m mainly) (Zhao *et al.* 2006), confirming the validity of method for local vegetation reconstructions. In terrestrial mire communities, the majority of seeds were derived from plants within 1 m radius (Greatrex 1983).

Plant macrofossil analysis is an important method to study LG environments and describe their vegetation composition. In LG, treeless landscape with low local pollen productivity (Davis and Deevey 1964), long-distance pollen rain, or resedimented pollen grains can easily lead to incorrect vegetation reconstructions based solely on pollen data (Birks and Birks 2000). The plant macrofossil data offers a possibility for validating and confirming/neglecting the results of pollen analysis. Another benefit of the plant macrofossil studies of the LG sediments is the possibility to use them as materials for radiocarbon dating. The use of terrestrial plant macrofossils for ^{14}C dating would diminish problems connected with the dating of bulk sediment materials, such as low organic carbon content, old carbon, and hard-water effects or contamination by roots (Wohlfarth *et al.* 1998, Birks and Birks 2000, Turney *et al.* 2000).

However, there are some features that affect the interpretation of plant macrofossil data in severe and barren environments. In severe conditions, vascular plants may not produce seeds but replicate vegetatively. Also, long-distance transportation over barren landscapes can lead to the accumulation of certain kinds of macrofossils into sediment layers, overestimating its role in vegetation composition. The migration and colonization rates during LG might have been inhibited by a high glacier melting rate as compared to the ability and strategy of different plant species to migrate. In Estonia, the estimated ice recession mean annual rate so far has been 110 m per year (Kalm *et al*. 2011). In modern glaciers, the rate is mostly much slower, several to tens of meters per year (e.g., Hodkinson *et al*. 2003).

3.3. History of Estonian plant macrofossil studies

The first notes on Quaternary palaeobotany, in particular about the LG macrofossils in Estonia, were made by the grand old man of Estonian geology, F. Schmidt, on an excursion around Estonia together with Swedish geologists A.G. Nathorst and N.O. Holst (Schmidt 1891). In Kunda, northern Estonia, above tills, they found remnants of arctic flora *Salix polaris*, *S. herbacea*, *Dryas octopetala*, *Polygonum viviparum*, cf. *Saxifraga caespitosa*, and *Betula nana*. In other places in Estonia, Livland, and the Vitebsk area, they confirmed these findings adding to the list *Salix reticulata* and concluded that the areas east of the Baltic Sea were once covered by arctic vegetation and not forests (Nathorst 1891).

However, the pioneer of palaeoecological studies in Estonia was P.W. Thomson, contemporaneous with the pioneer of pollen analyses L. von Post, who, besides compiling the first pollen diagrams in Estonia in the 1920s, was also interested in plant macrofossils (review in Kask and Raukas 1992, Thomson 1929). He also investigated LG sediment layers in Lithuania (Thomson 1931), describing open vegetation in Allerød and the "first spruce pollen in Russia," as he called it, and moss fragments from the Allerød layers. Since the 1960s, the radiocarbon dating method became more and more used for establishing timescales for geological and palaeoecological studies. Pollen and plant macrofossil data and ^{14}C datings from several localities were compiled to reveal the Holocene environmental history. Pollen analysis was prioritized, but H. and J. Allikvee (Ilves and Sarv 1969, Sarv and Ilves 1971) and analysts (U. Valk and others) from the Laboratory for Forest Research (Ilves *et al*. 1967, 1968, Ilves and Sarv 1970) also studied the plant macrofossils as botanical elements of sediment cores. For radiocarbon dating purposes only, botanical material was referred to as "plant detritus" (Punning *et al.* 1981), but sometimes, species names were also listed (Liiva *et al*. 1966). The plant macrofossils were frequently analysed in the context of peat studies as a natural mining resource by different governmental facilities (review in Orru *et al*. 2008, Veber 1965). Since the 1980s, more detailed studies on plant macrofossil assemblages in ancient archaeological localities (Kihno and Hiie 2008, Sillasoo 1997, 2005, Tammet 1988) or as natural archives for Holocene palaeoenvironmental research were carried out (Piiper 1988, Punning *et al*. 2004, Sillasoo *et al.* 2007, Vandel 2011).

Plant macrofossil studies from the LG period, though, have largely remained neglected in Estonia, perhaps for several reasons. One of them is probably the difficulty in gaining the LG sediment; in Estonia, typical LG sediments are mineral-rich (silts, clays, and varved clays) that are hard to penetrate with a hand-operated Russian corer. Also, plant cover in the LG period was scarce and therefore the production and thus the concentration of macrofossils per sample is low. The influx of mineral matter into sedimentary basins diluted the plant material, and due to that, rather large amounts of LG sediments are needed to gain sufficient plant macrofossil counts that are representative and reliable indicators of past vegetation. Additionally, most of the known sedimentary basins in Estonia – lakes and mires – started to accumulate plant material not before Preboreal. Therefore, finding suitable LG localities is another crucial question.

However, some remarks about macrofossils derived from LG sediments before this study are known. Thomson noticed spruce wood in the Kunda river outcrop sediment strata in northern Estonia, and he hypothesized it to be of LG origin (Thomson 1934). Pirrus (1969) photographed dwarf birch (*Betula nana*) leaves from an LG sediment core. These described the fragmentary findings accompanied by known locations of LG-buried organic layers, e.g., Kurenurme (Liiva *et al.* 1966) or Viitka (Punning *et al.* 1983), where sometimes, wood/plant detritus was collected for radiocarbon dating, comprise the rather short knowledge of LG flora in Estonia. Still, no systematic plant macrofossil studies, especially in conjunction with a chronological background, were performed before, thus evoking the idea of the current research work. In the present study, three LG sediment cores in Estonia and one in Latvia forming an N–S transect over the northern Baltic area were dated and analysed for plant macrofossils: Lake Udriku (Amon and Saarse 2010, Paper II), Lake Nakri (Amon *et al.* 2011, Paper III), Solova Bog (Amon *et al.* 2010, Paper I), and Lake Lielais Svētiņu (Veski *et al.*, manuscript, Paper IV).

4. MATERIAL AND METHODS

4.1. Study areas

Quaternary geology of eastern Baltic area

As part of the vast East-European Plain, the study area is characterized by a flat surface topography with small absolute and relative heights. The highest point of the area is the Suur-Munamägi Hill (318 m a.s.l.), which is situated in the Haanja Heights in the south-eastern part of Estonia. During the Quaternary Period, Estonia was repeatedly glaciated. Slightly

Figure 1. Location of study sites.

undulating plains dominate the topography (Raukas 2009). The Latvian relief is also rather flat, most of its territory lies below 120 m a.s.l. and the highest point is 312 m a.s.l. Estonian and Latvian topography has largely been shaped by Pleistocene glaciations, particularly of the last Weichselian event. Over a half of territory is a glacial lowland; most glacier uplands are insular-shaped and bedrock-cored (Zelčs and Markots 2004). The study sites are situated in northern Estonia (Lake Udriku), southern Estonia (Lake Nakri and Solova Bog) and eastern Latvia (Lake Lielais Svētiņu) (Fig. 1, Table 2a).

Floristic description of eastern Baltic area

The study area is located in the hemiboreal vegetation zone, within the transitional zone or ecotone (boreo-nemoral ecotone) between the two principal forest zones of Europe – boreal and nemoral zone. Peatlands and wetlands with specific floristic components are distributed over the whole territory (Masing *et al.* 2000). The zonal or climax vegetation type is boreo-nemoral coniferous forest: primarily Norway spruce (*Picea abies*) forest with silver birch (*Betula pendula),* aspen (*Populus tremula*), Scots pine (*Pinus sylvestris*), and to a lesser extent lime (*Tilia cordata*), ash (*Fraxinus excelsior*), mountain elm (*Ulmus glabra*) and oak (*Quercus robur*) in the tree layer (Laasimer 1965, Paal 1998). Due to the ecotonal nature of Estonia, many of the temperate tree species are close to their northern distribution limit (Seppä and Poska 2004). Aspen, grey alder (*Alnus incana*) and most silver birch (*Betula pendula*) forests are secondary in Estonia (Paal 1998). In Latvia, a phytogeographically important factor is the oceanity-continentality gradient that is responsible for a noticeable decline of flora in eastern Baltics (Rūsiņa 2007).

Climate

Estonia and Latvia are located between 56°N and 59.5°N at the eastern coast of the Baltic Sea in a transitional area from the maritime to the continental climate, characterized by a west–east gradient in the continentality of climate. Climatic conditions are determined mainly by high cyclonic activity and the prevalence of westerlies (Jaagus *et al.* 2010). The mean annual temperature in Estonia is 5.6 °C, seasonal variablity ranges from –4.0 °C (mean January temperature) to 16.7 °C (mean July temperature). The variability within country is more notable in case of winter temperatures (Jaagus 1997) when the difference of maritime West Estonia and more continental East Estonia is 4.8 degrees (–5.8 °C to –1.0 °C). Summer temperatures in Estonia are more even, ranging from 16.2 °C to 17.5 °C. Mean annual temperature in Latvia (Riga) is 7.2 °C, ranging from –1.6 °C (mean February temperature) to 17.7 °C in July (Krauklis and Draveniece 2004).

The mean annual precipitation in Estonia is 646 mm. Mean precipitation is lower in the coastal zone and increases toward hinterland (Jaagus *et al.* 2010). The snowcover in Estonia persists from December to late March. Mean value of snowcover duration varies from 75 days in the westernmost islands to more than 130 days in higher and forested regions in the north-east and south-east (Jaagus 1997). Mean annual precipitation in Latvia (Riga) is 681 mm (Krauklis and Draveniece 2004). A continuous snow-cover in Latvia forms at 8–29 December except the coastal territories in western Latvia where it is established during first decade of January (Draveniece 2009) and melts in March/April (Krauklis and Draveniece 2004).

Table 2a. The description of study sites.

	Lake Lielais Svētiņu	Solova Bog	Lake Nakri	Lake Udriku
Coordinates	56°45.5 N 27°08.8 E	57°42.024 N 27°24.915 E	57°53.703 N 26°16.389 E	59°22′17′′ N 25°55′50′′ E
Altitude, m a.s.l.	96	168	48.5	95
Size, ha	18.8	12	0.9	23.7
Water depth, m	4	–	3.2	4.8
Landscape	Glacial lowland; flat topography with elevations 96–101 m a.s.l.	Hummocky area in the eastern part of Haanja Heights; elevation 168 m a.s.l.	Slightly rolling glacial topography; local Otepää stage end moraine near the lake	NW slope of the Pandivere Upland; hummocky landscape with lowland patches
Modern vegetation	Birch forest	Drained and forested wetland (mixed forest)	Mixed conifer forest, fen	Mixed conifer forest

4.2. Methods

Sediment sampling

The investigated sites were selected to form a S–N directional transect over eastern Baltic area in order to capture the signal of vegetation development both LG in tundra and forested areas. Sediment cores were recovered from the deepest and most representative parts of the sediment basins, i.e. whereas the sediment thichkness was the largest. In some cases where the deepest cores were lacking macrofossils (Lake Pikkjärv, T. Hang unpublished) more littoral cores were used instead (Lake Prossa, Kihno *et al.* 2011).

Studied sediment cores were recovered using 7.5 and 10-cm diameter, and 1-m long Russian (Belarus) peat samplers. The lake sediments (Nakri, Lielais Svētiņu, Udriku) were cored from the lake ice surface in winter, Solova Bog was cored

Table 2b. The analytical methods applied and number of sample analysed.

Palaeoecological analyses	Lake Lielais Svētiņu	Solova Bog	Lake Nakri	Lake Udriku
AMS ^{14}C datings	12	7	9	4 + 2 unpublished
Plant macrofossils	77	25	93	31
Pollen	48	–	71	19 unpublished
Diatoms	28	20	30	10
Loss-on-ignition	311	110	503	179
Magnetic suseptibility	381	223	880	180
Grain size	–	–	–	19

during summer period. Sediment lithostratigraphy was described and the cores were photographed in field. The sediment was carefully packed into 1-m plastic semi-tubes, wrapped in polyethylene film, labelled and transported to the laboratory for further analyses (Table 2b).

Plant macrofossil analysis

The preparation for plant macrofossil analysis followed conventional procedures (Birks 2001). The sub-samples were determined by water displacement in a measuring cylinder. Samples were wet-sieved through 0.25 mm or 0.16 mm mesh. Clay-like sediment samples were soaked in $Na_4P_2O_7 \cdot H_20$ solution over several days to disintegrate fine-grained inorganic particles and to improve the ease of sediment sieving. Material retained on the sieves was examined using a stereo- and light microscope.

In case of Lake Nakri, the sample size was uniformly 100 cm^3. Lake Nakri sediment was divided into contiguous 2.5-cm intervals from more organic-rich sediments at core-depths of 1475–1500 cm and 1250–1304 cm and in contiguous 5-cm intervals from inorganic silty/clay-like sediments at core depths of 1510–1635 cm and 1304–1475 cm. In addition, three sub-samples were taken from the overlying gyttja at core-depths of 1226, 1201 and 1161 cm. The plant macrofossil analysis on Solova Bog was carried out in contiguous 4-cm intervals from sediment core in depth between 480–660 cm. The uniform sub-sample size (approximately 300 cm^3) was determined by displacement of water in a measuring cylinder. Macrofossils from Lake Udriku were extracted by soaking 5-cm thick samples (with a mean volume of 210–220 cm^3) in a water and $Na_4P_2O_7$ solution and then material was wet-sieved. In case of Lake Lielais Svētiņu, the sample size varied from 90 to 730 cm^3. The results from all study sites were recalculated to concentration (plant macrofossils per 1 cm^3) to ease the comparison.

Relevant literature and atlases (e.g. Beijerinck 1976, Berggren 1981, Anderberg 1994, Cappers *et al.* 2006) and reference collections (Institute of Biology, University of Bergen, Department of Environmental Archaeology, Danish Prehistory, The National Museum of Denmark, W. Szafer Institute of Botany, Polish Academy of Sciences) were used for plant macrofossil identification. In addition to plant macrofossils, several limnic organisms and stonewort (Characea) oospores (Amon 2010) remains were also identified and counted as well as moss remains from Lake Nakri and Solova Bog sediment cores.

In results, seeds of tree-type birch (*Betula pendula* and *B. pubescens*) were grouped as *Betula* sect. *Albae*. *Carex* seeds were divided into two groups by seed morphology: triangular seeds and lenticular seeds. Group *Drepanocladus sensu lato* sums up different *Drepanocladus* and *Warnstorfia* species. *Sphagnum* was also united into one group due to lack or detachment of stem leaves. The moss nomenclature follows that of Ingerpuu and Vellak (1998) and Abramov and Volkova (1998).

AMS radiocarbon datings

Plant macrofossils, which were identified during the course of macrofossil analysis, were radiocarbon dated by using the accelerator mass spectrometry (AMS) ^{14}C dating method in the Poznan Radiocarbon Laboratory (laboratory code: Poz), Poland. The material sent to dating laboratory was of terrestrial origin, e.g. debris of leaves, catkin bracts, twigs etc. The chronology of the sediment sequences were based on the weighted average calibration of AMS radiocarbon dates (0 BP = AD 1950), which were derived from the INTCAL dataset (Reimer *et al*. 2004, 2009). The dating results were fitted into the OxCal 4.1 (Bronk Ramsey 2001) deposition model (Bronk Ramsey 2008). Stratigraphic age estimates from ends of the deposition models were extrapolated. The age-depth models were built on weighted average modeled ages with error margins.

Loss-on-ignition and magnetic susceptibility

The organic matter content of the sediment was determined by loss-on-ignition (LOI) at 550 °C for 4 h (Heiri *et al*. 2001). The magnetic susceptibility (MS) was measured with a Bartington Instruments high resolution surface scanning sensor MS2E along carefully cleaned flat surfaces of fresh sediments covered by a thin plastic film with the resolution of 1 cm. The grain size distribution was analysed using laser scattering particle size distribution analyser Horiba LA-950V2.

Pollen

Pollen sample preparation followed a standard acetolysis method (Berglund and Ralska-Jasiewiczowa 1986) combined with cold 40% and/or hot 70% HF treatment to remove inorganic matter (Bennett and Willis 2001). *Lycopodium* spores were added to calculate pollen concentration, and subsequently, the pollen accumulation rate (PAR) values (Stockmarr 1971). Pollen data were expressed as percentages of the total terrestrial pollen sum, and PAR values were expressed as pollen grains cm^{-2} y^{-1}. Counts of spores, green algae, charcoal, and other microfossils were calculated as percentages of the total sum of terrestrial pollen.

Diatoms

Sediment sub-samples for diatom analysis were prepared from all investigated sediment records, however, diatoms were preserved only from the Holocene sediments of Solova Bog and in short LG sediment interval from Lake Lielais

Svētiņu record. In other sites sediments were devoid of diatoms. For diatom analysis freeze-dried sediment was weighted and the samples were digested in 30% H_2O_2 until organic material was oxidised. Few drops of 10% HCl were added to remove carbonates and thereafter the fine mineral particles were removed by repeated decantation. Commercially available divinylbenzene microscopic markers were added to determine diatom concentration. Few drops of cleaned sub-sample were dried onto cover glass and mounted on slides using Naphrax medium and analysed for microfossils under a Zeiss Imager microscope at × 1000 magnification using oil immersion and differential interference contrast optics. Diatoms were identified using standard floras and were grouped according to their habitat into planktonic and periphytic taxa, the latter including epipelic, epipsammic and epiphytic life forms.

Statistical methods and software applied

Macrofossil data was compiled using Tilia 1.0.1 (Grimm 2007). In case of Lake Udriku and Solova Bog, plant macrofossil zonation follows constrained incremental sum of squares cluster analysis (Grimm 2007). Lake Nakri and Lake Lielais Svētiņu macrofossil data was zoned based on the binary splitting of the sum-of-squares method using the PSIMPOLL 4.10 programme (Bennett 2002). The significance of statistically determined zones was estimated by comparison with the broken-stick model described by Bennett (1996). Statistical analysis of relations of PAR and plant macrofossil presence was performed with statistical analysis software R (version 2.12.2) (R Development Core Team 2011) using binomial regression analysis (Zuur *et al.* 2009). McFadden's pseudo R-square was calculated for characterize binomial model's goodness-of-fit measure.

5. RESULTS

5.1. Lithostratigraphy

The LG sediments comprised mostly silts, clayey silts and clays, sometimes laminated clays (Table 3). The organic matter content is generally low but rises in the Pleistocene/Holocene boundary.

5.2. Chronology

Results of the AMS radiocarbon dating are summarised in Tables 4a and 4b. The weighted average modelled ages are based on the deposition model in OxCal 4.1. (Bronk Ramsey 2001, Reimer *et al.* 2004). The ^{14}C datings are published in Amon and Saarse 2010 (Lake Udriku), Amon *et al.* 2011 (Lake Nakri), Amon *et al.* 2010 (Solova Bog) and Kihno *et al.* 2011 (Lake Prossa). The ^{14}C datings of Lake Lielais

Table 3. Lithostratigraphy of studied cores.

Depth, cm	Sediment description	LOI, %
	Lake Nakri	
320–1207	Gyttja, brown	9.9–29.5
1207–1240	Gyttja, distinctly laminated	13.3–29.9
1240–1262	Gyttja, coarse detritus, dark-coloured	12.3–33.2
1262–1464	Clayey silt/silty clay, beige, more organic rich in upper limit	2.0–10.3
1464–1500	Silt, dark-coloured, rich in diffuse organic matter	3.3–7.5
1500–1656	Silt, increasingly sandy towards bottom, beige	0.4–3.6
	Lake Udriku	
650–679	Gyttja, brown, dark	12.2–89.7
679–755	Silt, grey, greenish, rich in plant remains	5.5–11.3
755–780	Silt, grey, dark-coloured, indistinctly laminated	1.6–6.3
780–800	Silt, sandy, grey, dark, with few plant remains	2.6–9.9
800–828	Distinct laminations with alternation of silt, clayey, grey, dark and sand, fine, beige	0.8–3.7
	Lake Lielais Svētiņu	
1105–1160	Gyttja, silty, greenish brown, homogeneous	4.2–13.6
1160–1190	Silt, dark gray, with organic matter	3.6–6.8
1190–1268	Silt, gray, light	3.0–7.9
1268–1317	Silt, yellowish, with diffuse organic matter	3.3–6.3
1317–1332	Clay, distinctly laminated (varved clay?), ~20 lamina couplets	1.8–3.7
1332–1498	Silt, gray, increasingly dark-coloured towards the upper limit	1.5– 5.3
1498–1515	Sand, dark-coloured	1.9–3.2
1515–1535	Sand, beige, compact	1.9–2.5
	Solova Bog	
450–487	Gyttja, olive to green, homogeneous	17.0–82.0
487–516	Silt, greenish grey, with diffuse organic matter and plant detritus	4.0–12.6
516–560	Clayey silt/silty clay, grey	2.3–4.0
560–624	Silt, beige	2.1–2.9
624–637	Silt, clayey, light beige, massive	3.4–5.6
637–666	Silt with sandy interlayers, grey, indistinctly laminated	1.7–2.8
666–672	Sand, medium to fine-grained, grey, brownish	0.7–2.1

Svētiņu (Paper IV) and Raunis site are unpublished. Raunis dates are unmodeled calibrated dates calibrated by OxCal 4.1. Lake Prossa radiocarbon dates are calibrated with program Calib Rev 5.0.1 program (Stuiver *et al.* 2005). Lake Udriku datings are re-calibrated and modelled using OxCal 4.1 program, IntCal09 dataset (Reimer *et al.* 2009). The radiocarbon age estimation of basal part of Solova Bog sediment core was unexpectedly young due to insufficient amount of dated material and the date was rejected from chronology.

Table 4a. Radiocarbon dates from studied sediment sequences.

Depth below water, cm	Lab code	^{14}C date, y BP	Calibrated age, cal y BP	Dated material
		Lake Nakri		
1169	Poz-20611	8870±50	9970±125	Wood fragment, *Betula* seeds, *Betula* and *Populus* catkin scales
1241	Poz-20612	9610±60	11 105±65	*Betula* seeds, *Betula* and *Populus* catkin scales
1272	Poz-20076	10 150±50	11 610±125	Wood fragment
1422.5	Poz-22639	10 510±60	12 575±45	Wood fragment
1462	Poz-20077	10 800±40	12 830±20	Wood fragment
1497	Poz-20526	11 430±70	13 325±55	Terrestrial plant macrofossils
1520	Poz-20528	11 660±70	13 470±55	Terrestrial plant macrofossils
1545	Poz-20613	11 810±80	13 575±55	*Dryas* leaves
1630	Poz-20529	12 060±70	13 925±80	Terrestrial plant macrofossils
		Lake Udriku		
673	Poz-31429	10 190+50	11 700±290	Bulk gyttja
700	Poz-30769	10 060+60	11 950±200	*Dryas* leaves
745	Poz-30429	10 590+60	12 520±120	*Dryas* leaves
773	Poz-36168	11 240±100	13 040±170	*Dryas* leaves (unpublished)
803	Poz-30430	11 890+80	13 750±230	*Dryas* leaves
818	Poz-36201	12 090±80	13 920±160	*Salix polaris* leaves (unpublished)
		Solova Bog		
475	Poz-27810	9480±90	10 810±170	*Equisetum* macrofossils
500	Poz-27811	9930±50	11 370±105	*B. nana* twigs and catkin scales
512.5	Poz-27812	10 080±50	11 640±145	*B. nana* twigs, catkin scales and seeds
557	Poz-25210	11 660±60	13 515±85	Wood fragments
577	Poz-24058	11 900±60	13 765±70	B. nana twigs
636	Poz-22185	11 960±60	13 830±70	Wood fragments
657	Poz-25211	11 730±90		*Dryas* leaves (rejected dating)
		Lake Lielais Svētiņu		
1157	Poz-30426	10 100±60	11 620±20	Wood
1185	Poz-36710	10 270±50	11 990±90	Twigs
1215	Poz-31768	10 330±50	12 290±80	Wood
1261	Poz-31769	10 760±50	12 660±50	Twigs, bark
1315	Poz-36711	11 460±60	13 290±60	Bark
1355	Poz-36712	11 670±60	13 510±50	Stems
1365	Poz-36715	11 630±60	13 560±50	Twigs, *B. nana* leaves, *Potentilla* seed
1400	Poz-36713	11 840±60	13 740±50	Twigs
1445	Poz-36714	12 410±60	14 110±60	Twigs, *B. nana* leaf
1492	Poz-31770	12 380±60	14 220±100	Twigs, bark
1510	Poz-29298	12 420±60	14 350±110	Wooden material
1530	Poz-31771	12 350±60	14 520±210	Wooden material

Table 4b. Radiocarbon dates from additional Late-glacial sediment sequences.

Depth below water surface, cm	Lab code	^{14}C date, y BP	Calibrated age, cal y BP	Dated material
		Lake Prossa		
520	Poz-38460	7600±50	8400±35	*Dryas* leaves
530	Poz-35525	8690±50	9620±65	Terrestrial plant macrofossils
555	Poz-35466	10 710±50		Plant macrofossils (rejected dating)
575	Poz-38459	10 410±100	12 345±240	*Dryas* leaves
600	Poz-35467	11 650±50	13 500±80	Terrestrial plant macrofossils
625	Poz-35468	12 330±60	14 245±155	Terrestrial plant macrofossils
650	Poz-36169	12 380±70	14 370±205	*Dryas* leaves
		Raunis site		
490	Poz-38330	11 350±70	13 220±120	*Betula* sect. *Albae* twig
465	Poz-38331	11 420±60	13 280±105	*Salix polaris* twigs

5.3. Palaeobotanical analyses

In present thesis, main emphasis is on plant macrofossil analysis, therefore more detailed results of other palaeoecological methods could be found in publications (pollen analysis – Amon *et al.* 2011, Paper IV; diatom analysis – Amon *et al.* 2010, Paper IV; granulometric analysis – Amon and Saarse 2010).

Vascular plants

During palaeobotanical analysis, plant macrofossils of 33 taxa were found in sediments of Lake Nakri (Table 5a) and 25 taxa were found in samples of Lake Udriku (Table 5b). Sediments of Solova Bog (Table 5c) contained macroremains of 24 and Lake Lielais Svētiņu 30 different taxa (Table 5d).

Mosses

There are only limited studies of moss fragment analysis as a possible palaeoecological proxy from Scandinavia (e.g. Bennike and Hedenäs 1995, Jonsgard and Birks 1995) and some from Estonia. The latter are mostly dedicated to *Sphagnum* species (e.g. Koff 1986), mire/wetland humidity based climatic studies (e.g. Sillasoo *et al.* 2007) or peat studies (e.g. Aaviksoo *et al.* 1993, review in Orru *et al.* 2008). However, the richness of moss species and well-characterised recent ecological amplitude should encourage the use of moss analysis for LG palaeoenvironmental studies (Janssens 1990).

Table 5a. Lake Nakri plant macrofossil assemblages (MA).

MA (depth, cm)	Age, cal y BP	MA description
MA-5 1160–1256	11 350– 9800	Assemblage is characterised by (re)appearance of *Betula* sect. *Albae* and *Populus tremula* remains.
MA-4 1370–1256	11 350– 12 200	The species spectrum is dominated by cold-tolerating shrubs (e.g. *Betula nana*, *Salix polaris*) with variety of herbs (different grasses, *Saxifraga*, *Cirsium etc*.). *Dryas octopetala* re-appears ca. ~12 000 cal y BP. Telmatic and aquatic species (*Carex* types, *Eleocharis*, *Juncus*, *Selaginella*, *Potamogeton filiformis*, Characeae) are present constantly. At the end of zone a rise in amount of limnic organism remains (*Daphnia*, *Cristatella mucedo*) occurs. The species composition is similar to MA-3 but the abundance of macrofossils is higher.
MA-3 1370–1473	13 000– 12 200	The species composition consists of dwarf shrubs (*Betula nana*, *B. humilis*) and herbs (e.g. *Saxifraga*, *Rorippa*). Aquatic environment is characterised by one finding of *Potamogeton gramineus* and constant occurrence of Characeae oospores. *Plumatella* and *Cristatella* statoblasts are present in lower part of zone. The abundance of macrofossils is relatively low.
MA-2 1473–1515	13 450– 13 000	Species spectra consist of trees (*Betula* sect. *Albae*), dwarf shrubs (*B. nana*, *Salix*) and telmatic/aquatic plants (*Eleocharis*, *Juncus*, *Selaginella*, Potamogetonaceae, Characeae etc.). The abundance of limnic animal remains (especially *Cristatella mucedo*) is the highest. The first tree-type birch occurs at ~13 400 cal y BP.
MA-1 1515–1635	14 000– 13 450	The lowermost 20 cm of the sediment is barren of plant macrofossils. The dominating plant species found are *Dryas octopetala* and *Betula nana*. The rest of vegetation spectra consists of grasses, Saxifragaceae and *Carex* types.

Table 5b. Lake Udriku plant macrofossil assemblages (MA).

MA (depth, cm)	Age, cal y BP	MA description
MA-5 675–705	11 980– 11 700	Characteristic tundra plant, *Dryas octopetala*, disappears. Most of found plant macrofossils belong to aquatic species, especially to *Potamogeton* family.
MA-4 705–755	12 620– 11 980	The abundance of plant remains decreases. *Potentilla* seeds and telmatic plant (*Selaginella*, *Juncus*) remains are mostly found. In upper part of the zone the plant remain assemblage changes: *Nitella* oospores decline, while *Dryas octopetala* reappears.
MA-3 755–780	13 270– 12 620	The zone consists of 18 different taxa. *Dryas octopetala* leaves are dominant terrestrial plant macrofossils with variety of remains of herbs (*Papaver*, *Rumex*, Saxifragaceae etc.) and telmatic plants (*Eriophorum*, *Juncus*, *Luzula* etc.). A sudden rise in aquatic plant/algae abundance occurs (mainly *Batrachium*, *Potamogeton filiformis* and *Nitella* oospores).
MA-2 780–800	13 750– 13 270	The abundace of *Salix polaris* remains is decreasing in favour of another characteristic tundra plant *Dryas octopetala*.
MA-1 800–828	14 080– 13 750	The dominant species is *Salix polaris* whose leaves are main plant macrofossils found, in addition few seeds of *Silene* and *Batrachium* occur.

Table 5c. Solova Bog plant macrofossil assemblages (MA).

MA (depth, cm)	Age, cal y BP	MA description
MA-6 479–497	11 340– 10 960	Plant macroremains of tree-birch and *Alnus* are present. The variety of plant species grows remarkably (*Phragmites*, *Potamogeton natans*, *Chenopodium* spp., *Potentilla* spp. etc.)
MA-5 497–534	Hiatus in the lower part of zone	Characteristic tundra species as *Dryas octopetala* and *Betula nana* almost disappear while *Alnus glutinosa* appears. The amount of unidentified *Betula* seeds is growing. The richness of aquatic and telmatic plant spectra is increasing (*Potamogeton* family, *Ranunculus* sect. *Batrachium*, *Carex*, *Juncus*).
MA-4 534–557	Hiatus in the upper part of zone	At the lower boundary of the zone remains of *Betula pendula* (*B*. sect. *Albae*) is recorded. The number of plant macrofossils of shrubs (*Dryas*, *B. nana*, *Salix*), aquatic plants (*Potamogeton* family) and telmatic plants (*Carex*) is low.
MA-3 557–576	13 800– 13 545	The number of plant remains decreases. The abundance of *Dryas* and *B. nana* remains decline, the species richness of grasses and aquatic plants reduce, no herbs found.
MA-2 576–636	13 910– 13 800	The abundance of macrofossils increases. The species composition consists of shrubs (*Dryas*, *B. nana*, *Salix*), telmatic plants (*Carex*, *Eleocharis*, *Juncus*), few grasses, *Potamogeton* species and *Saxifraga* species. In the onset of the zone is an interval with no plant macrofossils.
MA-1 636–660	13 950– 13 910	The abundance of plant macrofossils is rather low. The spectrum is dominated by shrubs (*Dryas octopetala*, *B. nana*) and telmatic plants (*Juncus*, *Carex*). Aquatic plants are represented by *Batrachium* and Potamogetonaceae.

The moss remains were determined to species or family level from two studied localities: Lake Nakri (moss analysis results unpublished) and Solova Bog (Amon *et al*. 2010). Moss remains found were presented as presence/absence of species on the stratigraphic scale (Fig. 2).

In Lake Nakri, the moss groups present throughout the sediment core are *Drepanocladus sensu lato* and *Bryum* sp. Frequent finds are also remains of mosses of *Scorpidium* and *Calliergon* family. In the basal part of sediment core *Tomentypnum* is noticed and *Leskea* sp. is present in several samples. *Fontinalis* sp. occurs in upper part of sediment sequence.

In the Solova Bog, identified material from sediment section analysed for moss fragments (557–657 cm) consists mostly of widespread aquatic mosses in the lower part of sediment core. Upward in the core, succession of fen mosses and even more terrestrial species occurs. *Scorpidium scorpioides* is present throughout the given section; *Calliergon giganteum* is found in the lower half of the analysed sediment sequence. In the middle of the section is the first appearance of *Tomentypnum nitens* which is constantly present in upper part of the analysed

Table 5d. Lake Lielais Svētiņu plant macrofossil assemblages (MA).

MA (depth, cm)		Age, cal yr BP	MA description
MA-7 1140–1160		11 650–11 390	Zone is based on two samples that contain remains of conifer (*Picea*) and deciduous trees (tree-birch, aspen), no shrub macrofossils were recorded. Grasses (*Typha*) and *Juncus* are present.
MA-6 1160–1265		12 700–11 650	Pine and deciduous tree (tree-birch, aspen) macrofossil abundance drops quickly and vanishes in the start of the zone. In the lower part of the zone, the amount of plant macrofossils is low. In upper part of zone *Picea* macrofossils appear, dwarf birch and *Dryas* remains re-appear in the same layers. Telmatic (*Juncus*, *Carex*), aquatic (*Potamogeton*, *Hippuris*, *Batrachium*) and grasses are present.
MA-5 1265–1315		13 300–12 700	The assemblage changes quickly from birch forest to mixed conifer forest, dominant tree species are pine (*Pinus*) and tree-birch (*Betula*). *Populus tremula* is present. The number and species composition of aquatic species is stable (*Potamogeton*, *Zannichellia*, *Hippuris*). Telmatic plants, herbs and grasses are present (*Juncus*, *Carex*, grasses, *Saxifraga* etc.)
MA-4 1315–1405	MA-4b 1315–1350	13 500–13 300	*B. nana* disappears abruptly in favour of tree-birch (*Betula* sect. Albae). Telmatic plant remains are found in every sample. Herbs (*Saxifraga*, *Alchemilla*, Poaceae) and grasses are present.
	MA-4a 1350–1405	13 760–13 500	The majority of macrofossils of this subzone are *B. nana* leaves. *Dryas* is present in one sample. Few grasses and telmatic plant remains are found.
MA-3 1405–1490		14 200–13 760	The number of plant macrofossil declines. The amount of shrub and *Carex* remains decreases. *Dryas octopetala* and *B. nana* remains are present in most samples although in small numbers. Telmatic plants (*Selaginella*, *Carex*, *Juncus*) are present. The first appearance of Poaceae and *Saxifraga* plant macrofossils.
MA-2 1490–1515		14 400–14 200	Remarkable rise in abundance of plant macrofossils. Characteristic is abundance of *Betula nana* remains (leaves, seeds). Other shrubs present are *Salix polaris* and small quantity of *Dryas octopetala*. Wooden material is frequently found in samples. Telmatic plants are numerous (*Carex*, *Juncus*), *Potamogeton* spp. is present.
MA-1 1515–1530		14 500–14 400	The samples are barren or contain very few plant remains (*Carex* seeds).

sediment sequence. The only occurrence *Campylium stellatum* is in the middle of the analysed sediment core (approximately 13 850 cal y BP). *Tortula* is present in the upper part of the sequence.

Comparison of pollen accumulation rates and presence of plant macrofossils

The confirmation of the plant species' palaeo-presence on a local scale is mostly the result of plant macrofossil analysis. Empirical relationships based on modern analog studies from northern Finland have been developed to estimate the species'

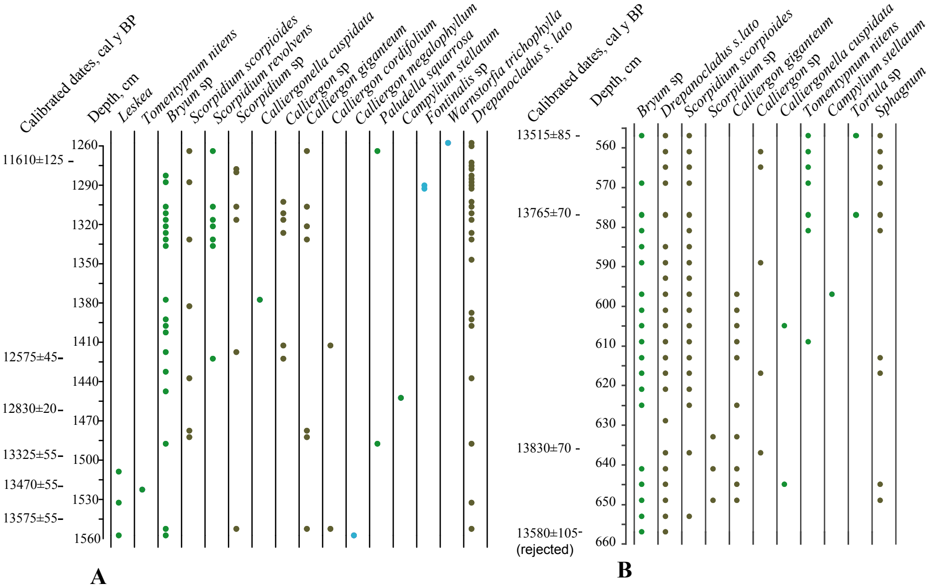

Figure 2. The moss species plotted against age and depth in (A) Lake Nakri and (B) Solova Bog. Aquatic mosses (blue); terrestrial mosses (green), present in both environments (brown) (according Ingerpuu and Vellak 1998).

presence based on PAR's (Hicks 2001, Seppä and Hicks 2006). Pine (*Pinus*) should be present when the PAR exceeds 500 cm^{-2} y^{-1} (Seppä and Hicks 2006). The PAR presence limits for birch and spruce are 500 and 50 grains cm^{-2} y^{-1}, respectively (Seppä and Hicks 2006). The PAR rate for the presence of pine forest is 1500 grains cm^{-2} y^{-1}; spruce and birch forest are locally present at PAR limits 100 and 1000 grains cm^{-2} y^{-1}, respectively (Hicks 2001). In principle, rise in (tree) pollen amount should preceed the occurrence of plant macrofossils as demonstrated by Paper II and Paper IV (Fig. 3). However, the relationships between PARs, plant macrofossils and presence of given species is not that straightforward: plant macrofossils of spruce could be present even in case of low amount of pollen (Väliranta *et al.* 2006). In addition, modern experiments show that modern tree line in Norway would not be detected by modern terrestrial pollen data while

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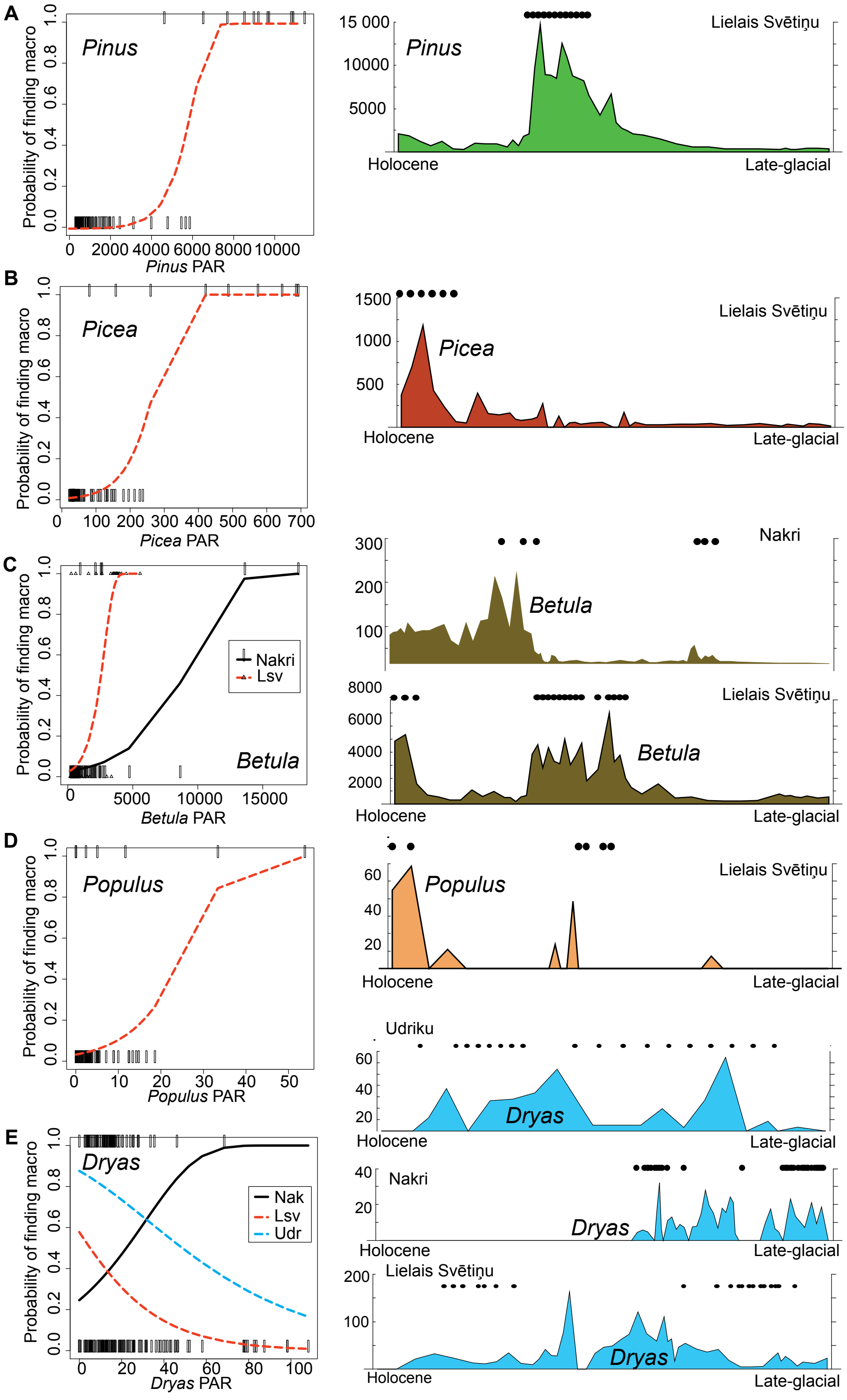
Figure 3. Plant macrofossil occurrence in comparison with pollen accumulation rates (PAR) based on binomial regression analysis (in left column) and plant macrofossil/pollen counts (in right column). In left column, the modeled probabilities of finding a macroremain of a given species is plotted against concurrent PAR. In right column, the given species counted PAR curve is plotted against counted macrofossils (dots). (A) *Pinus sylvestris*, (B) *Picea abies*, (C) *Betula* sect. *Albae*, (D) *Populus tremula*, (E) *Dryas octopetala*. Lsv – Lake Lielais Svetinu, Udr – Lake Udriku, Nak – Lake Nakri


A
Probability of finding macro
0.0
0.2
0.4
0.6
0.8
1.0
Pinus
0
2000
4000
6000
8000
10000
Pinus PAR
15 000
10000
5000
Pinus
Lielais Svētiņu
Holocene
Late-glacial
B
Probability of finding macro
Picea
0
100
200
300
400
500
600
700
Picea PAR
1500
1000
500
Picea
Lielais Svētiņu
Holocene
Late-glacial
C
Probability of finding macro
Nakri
Lsv
Betula
0
5000
10000
15000
Betula PAR
300
200
100
Betula
Nakri
8000
6000
4000
2000
Lielais Svētiņu
Betula
Holocene
Late-glacial
D
Probability of finding macro
Populus
0
10
20
30
40
50
Populus PAR
60
40
20
Populus
Lielais Svētiņu
Holocene
Late-glacial
Udriku
60
40
20
Dryas
Holocene
Late-glacial
E
Probability of finding macro
Dryas
Nak
Lsv
Udr
0
20
40
60
80
100
Dryas PAR
40
20
Nakri
Dryas
Holocene
Late-glacial
200
100
Lielais Svētiņu
Dryas
Holocene
Late-glacial

macrofossils represent local vegetation well (Birks and Bjune 2010).

The present study offered a possibility for comparing the findings of plant macrofossils with the studied species' PAR (Fig. 3). Five species were chosen for comparison: tree-birch (*Betula* sect. *Albae)*, pine (*Pinus*), aspen (*Populus*), spruce (*Picea*), and mountain avens (*Dryas octopetala*). The plant macrofossil sum does not contain stomatal data (counted during pollen analysis).

Pine macrofossils were found only in the Lake Lielais Svētiņu sediment samples. The probability of finding a pine macrofossil starts at 2000 grains cm^{-2} y^{-1} and exceeds 50% at the rate of approximately 6000 grains cm^{-2} y^{-1}. The model predicts that in case of over 7500 pollen grains cm^{-2} y^{-1}, a pine macrofossil should be surely present in the samples. The pseudo R-square is 0.88. Spruce (*Picea*) macrofossils were also found only in the Lake Lielais Svētiņu samples. The first rise in probability to find spruce macrofossils will occur at the rate of ~50 grains cm^{-2} y^{-1}. The PAR rate accompanying spruce macrofossils in the Lake Lielais Svētiņu samples is slightly over 400 grains cm^{-2} y^{-1}. The R-square value is 0.66.

Tree-birch (*Betula* sect. *Albae*) macrofossils were present in the samples of two study locations – Lake Nakri and Lake Lielais Svētiņu. The ratio of the plant macrofossil presence to the PAR value is different in those two sites. In Lake Lielais Svētiņu, a lower *Betula* PAR is found to predict the occurrence of macrofossils. Fifty percent possibility to encounter a tree-birch macrofossil requires a PAR limit of ~2500 grains cm^{-2} y^{-1}, while in Lake Nakri, 9000 grains cm^{-2} y^{-1} should be encountered. The unrealistic large PAR value in Lake Nakri is probably due to the scarcity of tree-birch macrofossils in the samples. The pseudo R-square value for the tree-birch binomial model is 0.57.

Aspen (*Populus*) was chosen as an example of species whose pollen is rarely found but its catkin scales are easily recognizable (Fig. 4). *Populus* catkin scales are found in the Lake Lielais Svētiņu and Lake Nakri sediments. The *Populus* PAR value of over 50 grains cm^{-2} y^{-1} should predict the presence of macrofossil findings. The pseudo R-square value for the model is low, 0.17.

The only herbaceous plant chosen for modeling was *Dryas octopetala*. The prediction about the relationship between plant macrofossils and PAR are controversial between study sites. At the Lake Nakri study site, the model predicts a positive relationship between PAR and macrofossil occurrence. However, in Lake Lielais Svētiņu and Lake Udriku, the relationship is negative; a higher PAR is coupled with a lower probability to find *Dryas* macrofossils. The possible explanation could lie in the pollen dispersal of *Dryas* in the environment and its stochastic presence in the sediments. In the surroundings of Lake Lielais Svētiņu, even the

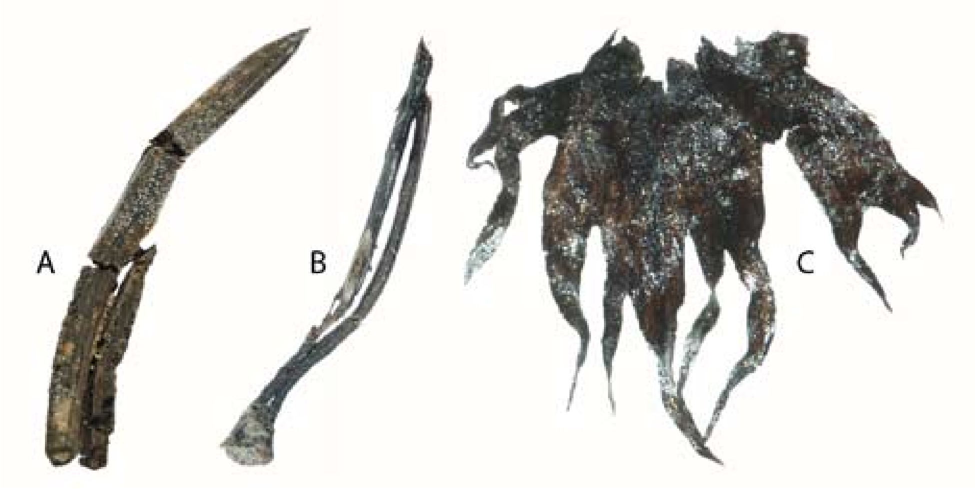


Figure 4. Photos of A. *Picea* needle (7x), B. *Pinus* needle (6x) and C. *Populus tremula* catkin scale (18x) from the Lake Lielais Svētiņu sediment profile at downcore sample depths of 1185, 1270 and 1290 cm, corresponding to ages of ca 12 000, 12 750 and 13 000 cal y BP.

amount of *Dryas* macrofossils is low in contrast to other study sites that indicate its low presence. Also, the surroundings of Lake Lielais Svētiņu were more close-forested that firstly diminished the possibility for *Dryas* pollen to disperse into the lake and secondly caused the domination of better dispersing of tree pollen in the pollen spectra. In the case of Lake Udriku, the surroundings were, on the contrary, very open and rather barren. In this case, the pollen probably dispersed rather stochastically. In conclusion, *Dryas* in the southern (forested) and northern (too barren) sites seem to act differently from the middle site, where the conditions were favorable for the *Dryas* pollen and macrofossil distribution.

6. DISCUSSION

6.1. Eastern Baltic floristic characterization and vegetation dynamics during the Late-glacial

The LG vegetation dynamics and chronology in Estonia have been a topic of discussion for several studies in recent years (e.g., Saarse *et al*. 2009, the articles included in the present thesis, Kihno *et al*. 2011), reopening the argumentation of LG vegetation dynamics and, as a byproduct, the debate on ice recession history. These studies present novel datasets about the palaeoenvironmental conditions based on pollen, plant macrofossil, and diatom or ostracod analysis with a series of AMS ^{14}C datings, providing a firm chronological control over the timescales.

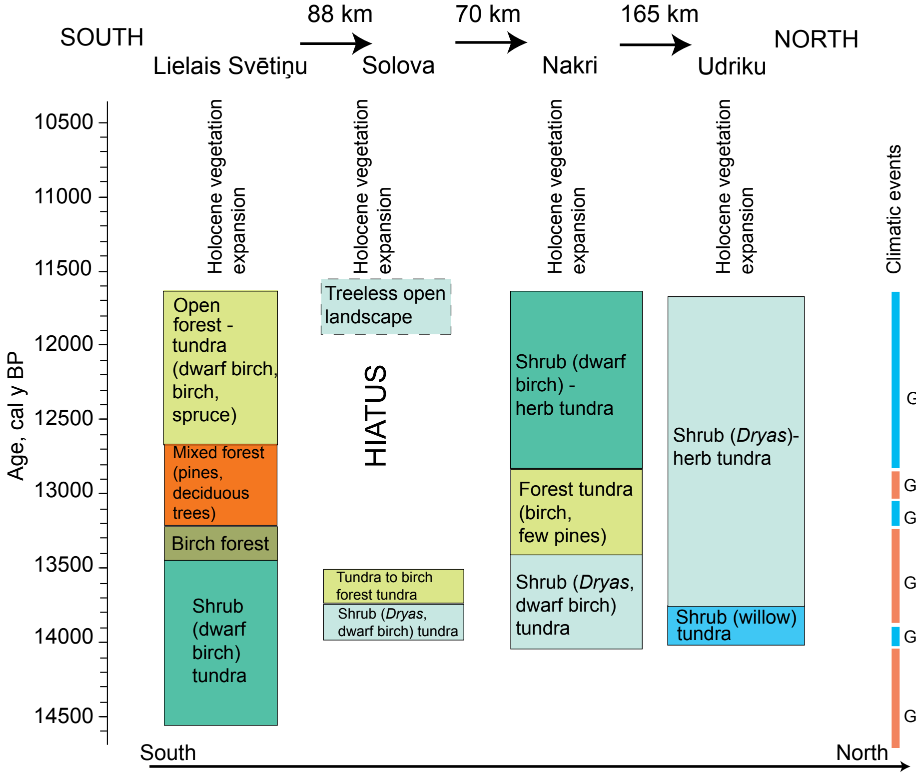


Figure 5. The dynamics of vegetation communities along S–N transect during Late-glacial period.

Several recent studies discuss LG vegetation in Latvia (Heikkilä *et al*. 2009, Ozola *et al*. 2010, Koff and Terasmaa 2011). All three studies carried out in Latvia combine pollen and plant macrofossil data. Unfortunately, the number of independent age estimations is low, and therefore, the time frame for a precise description of vegetation dynamics is modest. Heikkilä and co-authors presented few radiocarbon dates from Lake Kurjanovas and supported their chronology with biostratigraphic boundaries; however, they warned that the older part of chronology should be considered with caution (Heikkilä *et al.* 2009). In northern Latvian localities, two (Koff and Terasmaa 2011) or none (Ozola *et al*. 2010) radiocarbon datings were performed, leaving the chronology of vegetation dynamics vague.

The pattern of vegetation development in the eastern Baltic area, from eastern Latvia to northern Estonia (Fig. 5), follows a largely similar scheme during LG. With the occurrence of ice- and water-free land areas and suitable climatic conditions, the pioneer species migrated to glacier forelands and the treeless tundra communities dominated by shrubs and herbs/sedges established. The treeless tundra landscape extended from mid-Latvia during 14 500–13 500 cal y BP, southern Estonia during 14 000–13 500 cal y BP, and it persisted in the northern part of Estonia until the start of Holocene. The vegetation on the Lubana glacial foreland (Paper IV) was rather scarce during the pioneer phase: only two seeds of *Carex* were found and the pollen spectra contained a number of pollen grains of redeposited thermophilous trees (*Alnus*, *Corylus*, *Carpinus*, *Quercus*, and *Ulmus*, in total, 20%) of which large amounts (over 70%) were corroded. The landscape was without biological legacy, facilitating the migration species and barren as demonstrated by the high values of MS due to erosion. The organic matter content stays below 2.5%.

The ameliorating climatic conditions during phase GI-1e (in older scientific literature, the first described postglacial stable period is often named "Bølling"), though, allowed the pioneer community to be replaced with stable and more species-rich vegetation type in ~100 years. Judged on plant macrofossil data, the treeless tundra community consisted of shrubs (*Betula nana*, *Dryas octopetala*, and *Salix polaris*) and telmatic plants (*Carex* and *Juncus*). This period includes a sediment interval with a surprisingly high amount of plant macrofossils, hinting at a rather productive community supported by suitable climatic and environmental conditions. Another reason might be the openness of the landscape that favored fast transportation of plant remains into the lake (Glaser 1981) and therefore good preservation in the sediment records. The average MS value for this sediment interval is >23 10^{-5} Si units that confirms the active erosion from catchment. In the second part of Bølling, the dwarf birch–sedge assemblage was replaced with a dwarf birch and *Dryas* assemblage; a decrease in the number of plant remains occurred.

The pollen record shows that the PAR of birch reaches over 500 and up to 800 grains cm^{-2} y^{-1} by the end of the warm period at 14 200 cal y BP that should mark the local presence of the tree-birch (Seppä and Hicks 2006). A binomial model on the relationship of the *Betula* pollen and macrofossil (Fig. 3) shows that birch PAR should be ~1400 grains cm^{-2} y^{-1} with 20% probability of encountering a macrofossil and ~2500 cm^{-2} y^{-1} with 50% probability; therefore, it is no surprise that tree-birch macrofossils are absent in samples. The tree-*Betula* macrofossils dated to ~14 700 cal y BP were found in the Lake Kurjanovas sediments (Heikkilä *et al.* 2009); however, the age estimate is disputable.

The GI-1d or "Older Dryas" in early Baltic literature was a short cooling episode, ~125 years according to the Greenland ice core data (Lowe *et al.* 2008), before the GI-1c warmer climatic episode. By this time, all study localities were already deglaciated and the first plant macrofossils were deposited, although in small amounts (Fig. 6). The plant macrofossil evidence confirms the prevalence of treeless tundra conditions during GI-1d in the eastern Baltic area although with different dominant species (Figs 5, 7, 8) indicating a change in environmental conditions.

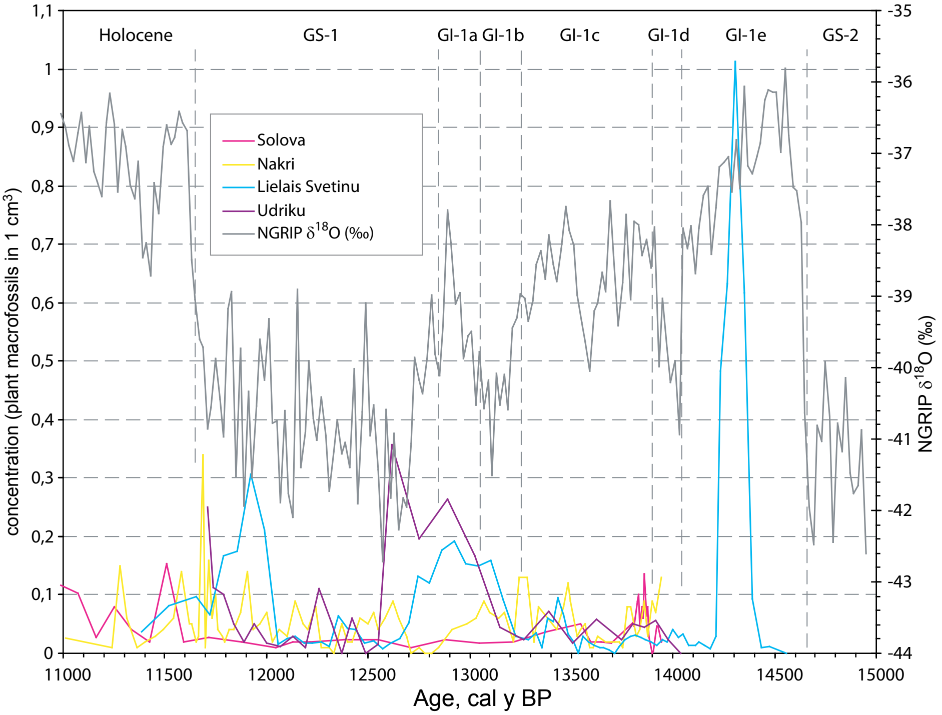


Figure 6. The plant macrofossil concentration in studied Late-glacial sediments plotted against timescale and NGRIP $\delta^{18}O$ (‰) data (Rasmussen *et al*. 2006).

In eastern Latvia, the *B. nana–Dryas* tundra is enriched with new grass and forb species (*Saxifraga aizoides* and Poaceae), indicating drier growth conditions than those during Bølling period. The treeless shrub tundra community also prevailed in all other study locations but with a higher proportion of *Dryas* in southern Estonia (Fig. 8) and that of *Salix polaris* tundra in northern Estonia (Figs 5, 7). The differences in species composition can also be interpreted to represent the environmental gradient along the transect from the glacier foreland in northern Estonia to the areas with established land cover in eastern Latvia. Erect dwarf shrubs such as *B. nana* are favored by higher growing season temperatures (minimum mean July temperature 7 °C, Isarin and Bohncke 1999) and usually appear during the later successional stages (CAVM Team 2003). Prostrate dwarf shrubs such as *Dryas* and *Salix polaris* are less demanding, and as early successional species they usually migrate earlier to the recently deglaciated areas and tolerate harsh climatic conditions. *Dryas* is common in drier ridge localities on alkaline or circumneutral substrates (Elvebakk 1994). *Salix polaris* is a late snowbed species on circumneutral and alkaline substrates in Fennoscandia (Dahl 1986, Elvebakk 1994). It suggests that the snow cover persisted longer in the northern part of the study area, indicating harsher climatic conditions nearby the

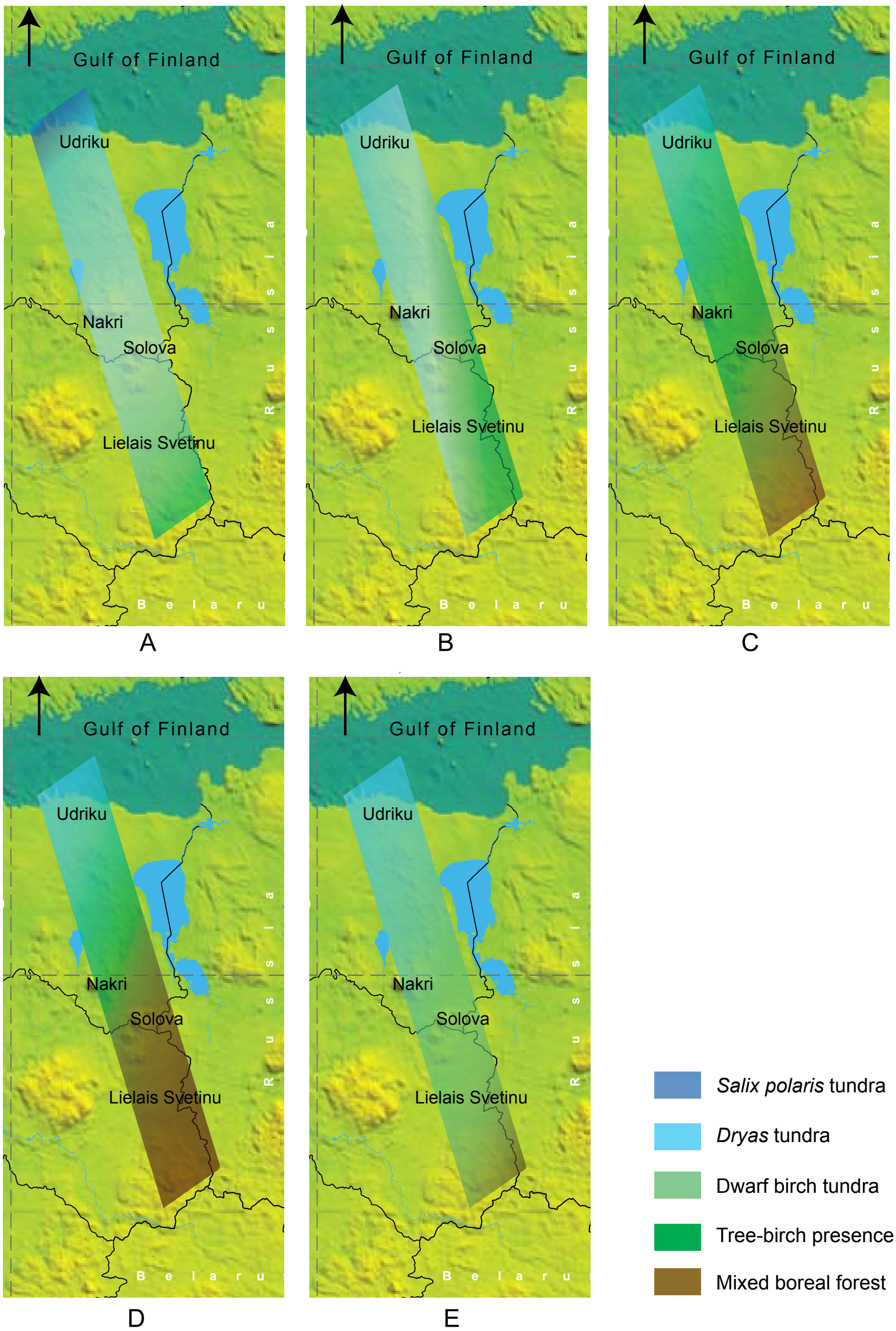


Figure 7. The schematic vegetation dynamics in eastern Baltic area in Late-glacial period. (A) GI-1d; (B) GI-1c; (C) GI-1b; (D) GI-1a; (E) GS-1. The SE-NW transect reveals the vegetation movements and reaction to climatic events. In southern section of study area, the vegetation is more prone to react to environmental changes while in northern part the vegetation consist of treeless tundra community during Late-glacial period.

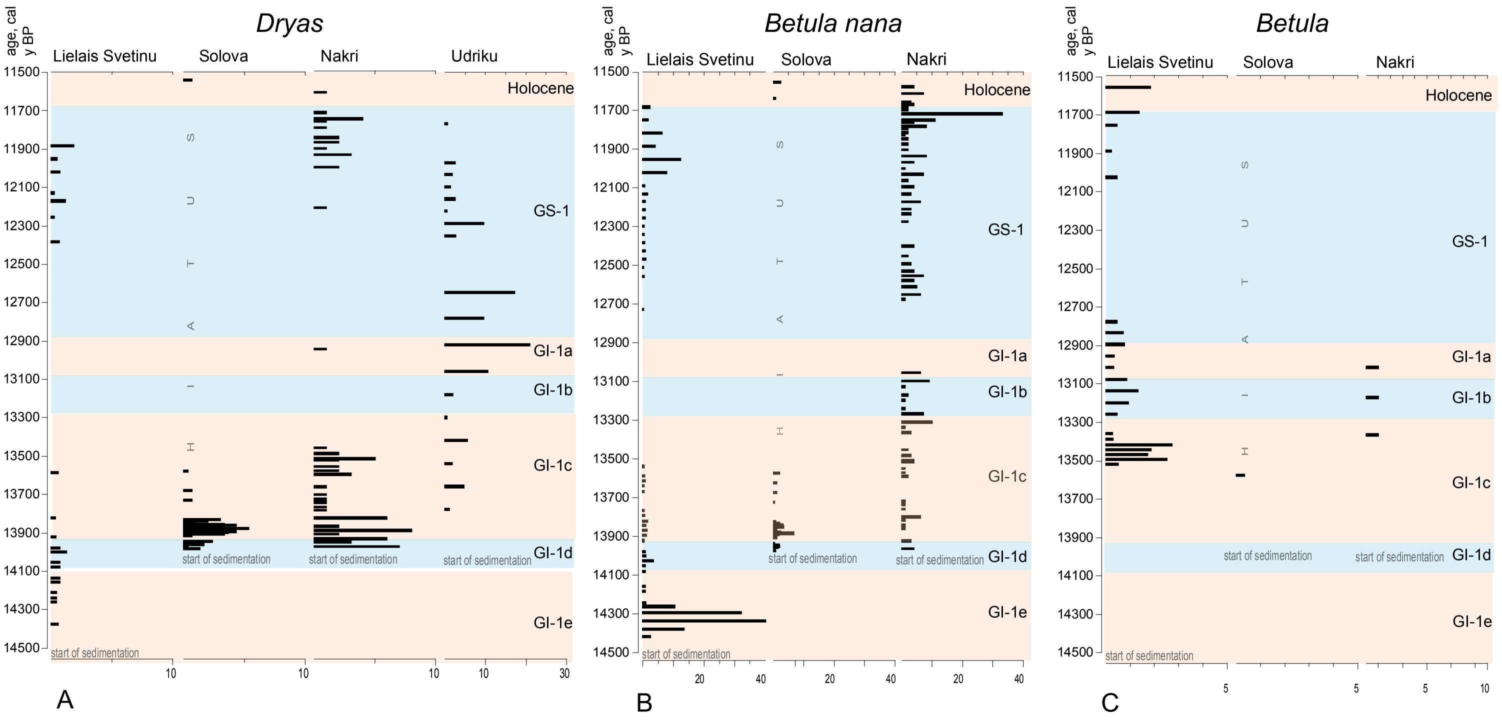


Figure 8. Comparison of the occurrence of selected macrofossils at study sites (Lake Lielais Svētiņu, Solova Bog, Lake Nakri, Lake Udriku).
(A) presence of *Dryas octopetala* macrofossils along S–N transect.
(B) presence of *Betula nana* macrofossils along S–N transect (not present in Lake Udriku)
(C) presence of *Betula* sect. *Albae* macrofossils along S–N transect (not present in Lake Udriku).

glacier (Figs 5, 7, 8).

The introduction of the GI-1c warming episode made the climatic conditions suitable for vegetation expansion and led to the gradual development of forests in the southern part of the eastern Baltic. The dwarf birch tundra was replaced with the low shrub tundra, indicated by the presence of *Betula humilis*; however, this community was rapidly replaced with birch forest, indicating the arrival of treeline in the eastern Baltic area (Fig. 7). The appearance of trees and the formation of treeline is a clear sign of succession from arctic to boreal environment. The treeline advances and fluctuations during LGM and afterward in Europe and northeastern European Russia have been discussed in several recent publications (Willis and van Andel 2004, Birks and Willis 2008, Binney *et al.* 2009, Väliranta *et al.* 2010). The trees survived the LGM in the refugial areas; however, the locations of those sheltered sites are under debate (Willis and van Andel 2004, Birks and Willis 2008). The plant macrofossil evidence places the refugias not only in southern and central Europe but also near the ice front in Russia (Väliranta *et al.* 2010) and Norway (Kullman 2008).

The first tree species recorded in the eastern Baltic area during LG is tree-birch (group *Betula* sect. *Albae* consisting *B. pendula* and *B. pubescens*). Based on *Betula* sect. *Albae* macroremains, the tree-birch reached ~13 500 cal y BP surroundings of Lake Lielais Svētiņu. The treeline advanced rapidly northwards: the first tree-birch macrofossils found in southern Estonia occur about the same time, i.e., at ~13 500 cal y BP (Solova Bog) and ~13 350 cal y BP (Lake Nakri). The older age of tree-birch macroremains in Solova Bog might be misinterpreted as a result of imprecise dating/modeling of the timescale. The postglacial expansion nuclei for tree-birch in the eastern Baltic area are difficult to distinguish, but tree-*Betula* was present more than 14 300 cal y BP in Lithuania (Stančikaitė *et al.* 2008) and >13 800 cal y BP in central Belarus (Novik *et al.* 2010). Based on these age estimations the rate of migration of birch from Lithuania to Latvia was 130 m y^{-1} and from Latvia to southern Estonia 800 m y^{-1}.

The rapid migration and development of mixed forest in eastern and mid-Latvia took place ~13 400–12 700 cal y BP, during GI-1e and GI-1c (Heikkilä *et al.* 2009). The general trend is that tree birch arrives first and forms open forests and pine arrives later, expands at the expense of birch, and becomes a dominant forest-forming species through the GI-1c/GI-1a periods. The situation is somewhat similar to the early Holocene Preboreal vegetation succession and forest development, with the difference of a stronger LG herb signal. The pine presence during Allerød in the eastern Baltic area is confirmed in the surroundings of Lake Lielais Svētiņu and Lake Nakri. The first stomata of pine from Lake Lielais Svētiņu date back to 13 450 cal y BP, while other macrofossils (Fig. 4) were found later (bark 13 300–12 700 cal y BP, needles 13 100–12 700 cal y BP). In Lake Nakri, the pine presence is hinted at by the finding of single stomata (13 300 cal y BP). Pine was present in Belarus during pre-LGM and had its refugia in western Russia during LGM (Binney *et al.* 2009). Southwards from the eastern Baltic area, *Pinus sylvestris* was present ~14 000 cal y BP in Lithuania (Stančikaitė *et al.* 2008) and >13 800 cal y BP in Belarus (Novik *et al.* 2010). Pine macrofossils, dating back to 15 000–13 000 cal y BP, have been found in Belarus and east of the Gulf of Finland (cf. Binney *et al.* 2009). However, no spruce macrofossils, stomata or a remarkable quantity of pollen was found in contrast to one *Picea* budscale present in the Lake Kurjanovas sediments during GI-1e/GI-1c (Heikkilä *et al.* 2009). In the northern part of the study area, the *Salix polaris* tundra was replaced with *Dryas*-dominated tundra with grasses, suggesting open but less moist surroundings (Fig. 7).

The GI-1b short cooling (so-called Gertzensee oscillation) did not cause any significant depauperation of terrestrial flora, as reflected by plant macrofossils. The plant macrofossil concentration is rather high in most of the study locations (Fig. 6). In the southern part, mixed conifer forest prevailed. Around Lake Udriku, treeless tundra prevailed with a domination of *Dryas* (Figs 7, 8) and the presence of grasses and different herbs (*Rumex* and *Saxifraga oppositifolia*), confirming dry surroundings. However, the Gerzensee cold event centered at 13 150 cal y BP is recognized in the aquatic signal of the Lake Lielais Svētiņu record as a remarkable decrease in the accumulation rate (AR) of Cladoceran remains, AR of *Pediastrum* and *Scenedesmus*, and diatom concentration. The life cycle of aquatic organisms in arctic lakes is dependent on climate related variables, e.g., the duration and extent of ice cover (Douglas and Smol 1999). During colder and longer winters, a thick ice cover probably formed, which delayed the break-up of lake ice in the deeper areas, and only the narrow areas in the littoral zone were ice-free.

The GI-1a warming is reflected by the increase in macrofossil concentration in Lake Lielais Svētiņu and Lake Udriku but its decrease in Lake Nakri (Fig. 6). The dominance of mixed boreal forests continued in the southern part of the eastern Baltic area (Fig. 7). The mixed forest in Lake Lielais Svētiņu area incorporated, besides pine and birch, also aspen (*Populus tremula*, Fig. 4), which immigrated during GI-1a. The presence of *Hippophaë* is suggested by pollen record as well. Findings of spruce wood and spruce pollen dated to the described period (12 900 cal y BP) were reported in Lake Kuži (Koff and Terasmaa 2011).

GS-1 or Younger Dryas cooling (Lowe *et al.* 2008) reintroduced harsher climatic conditions that repelled warmth-demanding species from the eastern Baltic area to more favorable regions, and the arctic and alpine vegetation spread southwards once more. The plant macrofossil concentration decreased sharply in Lake Lielais Svētiņu and Lake Udriku (Fig. 6). The forests declined in favor of the open tundra landscapes (Figs 5, 7). In general, the vegetation in the whole study area reacted to changing climatic conditions ~12 800 cal y BP. The dominant vegetation components were shrubs, sedges, and grasses. At the end of GS-1 cooling, another rapid change took place in the southern part of the study area. At 11 950 cal y BP, the community of dwarf shrubs, grasses, and spruce became prevalent. Spruce was introduced to the Lake Lielais Svētiņu area earlier, confirmed by the first stomata and rise in the pollen concentration at 12 400 cal y BP and *Picea* macrofossils at 12 000 cal y BP (Fig. 4A). The combination of fossil pollen and the genetic data of *Picea abies* reveal the LGM refugium area in the Russian Plain that became the basis of the so-called northern lineage of the present spruce in northern Europe (Giesecke and Bennett 2004, Latalowa and van der Knaap 2006, Tollefsrud *et al.* 2008). Plant macrofossil data support the *Picea* continuous presence in north-east European Russia more than 12 000 cal y BP (Väliranta 2005), even in case of very low pollen counts (Väliranta *et al.* 2006). Younger Dryas spruce was also found in eastern Latvia (Heikkilä *et al.* 2009); however, in the area of Lake Burtnieki, no spruce macrofossils were found (Ozola *et al.* 2010).

In southern Estonia, the tundra community without any conifers turned step-by-step into the forest, including the reappearance of deciduous trees (*Betula*, *Alnus* and *Populus tremula*) and a larger variety of herbs, grasses, and sedges at Pleistocene/Holocene boundary.

In northern and northeastern Estonia, vegetation was more modest as judged by the plant macrofossil record of Lake Udriku, Lake Äntu Sinijärv, and Lake Kaarepere Pikkjärv (Fig. 9). In the sediments of Lake Udriku, only some *Dryas* and few telmatic plant remains are found, suggesting barren and sparsely vegetated landscape. In Lake Äntu Sinijärv (Laumets *et al.* in prep.), the species spectra consist of *Dryas* and *B. nana*. The openness and erosion on the Lake Äntu Sinijärv shores is hinted by the large accumulation of *Dryas* leaves in the basal layer of the sediment core. Lake Kaarepere Pikkjärv (T. Hang, unpublished) on the Saadjärve Drumlin Field contains almost no plant macrofossils at all, but few *Dryas* leaves confirm that the sedimentation started in the LG period.

6.2. Late-glacial climate change

Climatic conditions (temperature, precipitations, etc.) are the main limiting factors for vegetation composition and dynamics. The present study often refers to hemispheric-scale climate events of the LG period. These events are relatively well studied, and generally, accepted information is gained by the synchronization of ice-core, marine, and terrestrial palaeorecords (Lowe *et al.* 2008). Palaeoecological methods for reconstructing local or regional temperatures of the LG period are, for example, based on pollen (Velichko *et al.* 2002, Seppä *et al.* 2008), beetle (Coope *et al.* 1998), or chironomid (Bedford *et al.* 2004, Heiri *et al.* 2007) records. For the LG period, the pollen-based temperature reconstruction is a challenge due to the low local pollen production, distant pollen in spectra, as well as the occurrence of "non-analog" pollen assemblages that are difficult to interpret based on the principle of actualism (Birks and Seppä 2010). The addition of plant macrofossil data would confirm the local presence of the given species. Moreover, most plant macrofossil assemblages can be readily interpreted in terms of modern arctic or alpine communities (Birks 2008).

Plant fossil record-based approaches used for palaeoenvironmental reconstructions are commonly looking at either specific indicator species with characteristic climatic preferences (e.g., Isarin and Bochnke 1999, Birks and van Dinter 2010) or ecological indicator values (Mortensen *et al.* 2011). The ecological indicator values are widely used in modern plant ecology studies. However, most of the commonly used indicator values are derived from Germany (Ellenberg *et al.* 1991) and Switzerland (Landolt *et al.* 1977) and therefore are best applicable to mid-European conditions. The results of macrofossil analysis, reflecting a local rather than regional vegetation composition, are often difficult to interpret in terms of regional climatic conditions. However, studies using macrofossil data as a basis for contemporary temperature reconstructions, exploiting the indicator species and/or assemblages approach, are available (e.g., Birks and van Dinter 2010).

Bearing in mind that plant macrofossil analysis is able to reveal the dominant components of past flora (Zhao *et al.* 2006), the cautious parallels with modern arctic vegetation units (CAVM Team 2003) could be drawn to ease the reconstruction of environmental conditions. One of the limiting factors for modern vegetation dynamics in arctic areas and glacier forelands is temperature. The modern bioclimatic zones, usually differentiated using temperature-based climatic parameters (per ex. mean annual temperature, warmest month's temperature, coldest month's temperature, or number of growing-degree days), are an example of vegetation classification based on the information of plant species' temperature preferences. The bioclimatic envelopes of vegetation zones might be referred to as landmarks for establishment conditions and temperature-tolerance limits for specific plant communities. Although the climatic conditions during the LG period were unique and do not have direct modern analogs, the bioclimatic envelope of plant species or communities could not be much different from those we observe today. Therefore, the tentative reconstruction of contemporary temperatures can be made based on the knowledge of modern bioclimatic variables typical for vegetation zone where observed species or communities co-exist.

The chironomid-inferred July temperatures from Lake Nakri, southern Estonia (Kirilova *et al.* 2011) estimate ~12 °C around 14 000 cal y BP (GI-1e/GI-1d). The signals of Allerød warming are relatively modest and temperature reconstruction shows a rise by 1 °C to 13 °C. During Younger Dryas cooling, the July temperature decreased to 10.7 °C. The pollen based summer temperature calculations (Velichko *et al.* 2002) based on pollen records from different localities, including Visusti in Estonia (Pirrus 1971), show somewhat higher temperatures during Allerød and agree well with the chironomid-inferred results for the Younger Dryas cooling period (Table 6a-d).

The taxonomic composition of differentiated plant macrofossil assemblages was compared with that of modern arctic vegetation units derived from CAVM Team (2003) in order to allocate the closest modern vegetation analog (Table 6a-d). The comparison with CAVM Team (2003) gave the best results for Lake Udriku where relatively stable vegetation composition, characterized by treeless tundra, existed throughout the LG period. The macrofossil assemblages comprising tree species remains were not comparable with the CAVM units as arctic communities are defined to be treeless (above treeline). The arctic treeline, according to Tuhkanen (1993), is determined by over a 10 °C mean temperature of the warmest month's isotherm. This statement coincides well with the CAVM Team (2003) suggested treeline mean temperature of the warmest month's isotherm between 10 and 12 °C. The tree species temperature tolerance is often characterized by the winter temperatures. These are (review in Willis and van Andel 2004) tree-*Betula* (–40 °C), *Pinus sylvestris* (–40 °C), *Picea abies* (–17 °C), and *Populus tremula* (–40 °C); or (review in Miller *et al.* 2008) tree-*Betula* (–30 °C), *Pinus sylvestris* (–30 °C), *Picea abies* (–30 °C), and *Populus tremula* (–30 °C). For spruce, the southward distribution limits the isotherm of the coldest month to –2 °C (Dahl 1998). According to Odland (1996), the distribution of the treeline-forming tree birch in Scandinavia follows a 13.2 °C isotherm for summer temperature.

The bioclimatic zones determined based on plant macrofossil assemblages in eastern Baltic during the LG are C, D, and E, according to the CAVM Team (2003) and the boreal forest. The first subzones A and B distinguished by the CAVM Team (2003) are not differentiable by the investigated fossil macrofossil data. The reasons for this can be found in the combination of the scarcity of initial plant cover, as in the case of modern glacier forelands, the increased size of the sedimentary basin due to glacial melt-water-fed proglacial waterbodies, and the high sedimentation rates leading to a low concentration of organic matter in sediment samples. Zones C and D refer to the prostrate to erect dwarf shrub tundra units, and zone E represents the low shrub tundra to the treeline communities. Zone C is present in the northern part of the study area, while in the southern areas, D and E zones were distinguished (Table 6a-d).

The succession of the determined bioclimatic zones generally follows the established pattern of climatic episodes and vegetation dynamics (Figs 5, 7). The Allerød warming is reflected by a warmer bioclimatic zone while the Younger Dryas (GS-1) cooling led to the return of the communities characteristic to colder zones. The temperature estimates characteristic to modern bioclimatic zones and

Table 6a. Lake Udriku plant macrofossil assemblages (MA), possible correlation to modern tundra vegetation zones (CAVM Team 2003), correlation to bioclimatic zones (Walker *et al*. 2005) and different temperature estimations (Walker *et al*. 2005, Velichko *et al*. 2002, Kirilova *et al*. 2011).

MA (depth, cm)	Age, cal y BP	Possible correlation to modern tundra vegetation zones (CAVM Team 2003)	Correlation to bioclimatic zones (Walker *et al.* 2005)	Estimated plant cover % (Walker *et al.* 2005)	July T °C based on bioclimatic zones (Walker *et al.* 2005)	NGRIP events (Lowe *et al.* 2008)	Pollen based mean July T °C estimation in eastern Baltic (Velichko *et al.* 2002)	Chironomid based mean July T °C estimation in eastern Baltic (Kirilova *et al.* 2011)
MA-5 675–705	11980–11700	G2 Graminoid prostrate dwarf-shrub forb tundra	C, zonal	5–50%	5–7	Younger Dryas/ GS-1	~10.7	~10.7
MA-4 705–755	12620–11980							
MA-3 755–780	13270–12620	G3 Nontussock sedge dwarf-shrub moss tundra	D, moist to dry, ridge	50–80%	7–9	Allerød/ GI-1a–1c	~15.7	~13 (13700–12850 cal y BP)
MA-2 780–800	13750–13270							
MA-1 800–828	14080–13750	G3/P2 Nontussock sedge dwarf-shrub moss tundra	C, moist, zonal	5–50%	5–7			~12 (14000–13700 cal y BP)

Table 6b. Lake Nakri plant macrofossil assemblages (MA), possible correlation to modern tundra vegetation zones (CAVM Team 2003), correlation to bioclimatic zones (Walker *et al*. 2005) and different temperature estimations (Walker *et al*. 2005, Velichko *et al*. 2002, Kirilova *et al*. 2011).

MA (depth, cm)	Age, cal y BP	Possible correlation to modern tundra vegetation zones (CAVM Team 2003)	Correlation to bioclimatic zones (Walker *et al*. 2005)	Estimated plant cover % (Walker *et al*. 2005)	July T °C based on bioclimatic zones (Walker *et al*. 2005)	NGRIP events (Lowe *et al*. 2008)	Pollen based mean July T °C estimation in eastern Baltic (Velichko *et al*. 2002)	Chironomid based mean July T °C estimation in eastern Baltic (Kirilova *et al*. 2011)
MA-5 1160–1256	11350–9800	Boreal forest	Boreal forest	100	>10–12			
MA-4 1256–1370	11350–12200	G4 Dwarf shrub graminoid tundra	D	50–80	7– 9	Younger Dryas/ GS-1	~10.7	~10.7
MA-3 1370–1473	13000–12200	S2 Low-shrub tundra	E	80–100	9–12			
MA-2 1473–1515	13450–13000	S2 Low-shrub tundra/boreal birch forest	E/birch treeline	80–100	>10–12	Allerød/ GI-1a–1c	~15.7	~13 13700–12850 cal y BP ~12 14000–13700 cal y BP
MA-1 1515–1635	14000–13450	G4/W2 Dwarf shrub graminoid tundra/wetland	D	50–80	7–9			

Table 6c. Solova Bog plant macrofossil assemblages (MA), possible correlation to modern tundra vegetation zones (CAVM Team 2003), correlation to bioclimatic zones (Walker *et al.* 2005) and different temperature estimations (Walker *et al.* 2005, Velichko *et al.* 2002, Kirilova *et al.* 2011).

MA (depth, cm)	Age, cal y BP	Possible correlation to modern tundra vegetation zones (CAVM Team 2003)	Correlation to bioclimatic zones (Walker *et al.* 2005)	Estimated plant cover % (Walker *et al.* 2005)	July T °C based on bioclimatic zones (Walker *et al.* 2005)	NGRIP events (Lowe *et al.* 2008)	Pollen based mean July T °C estimation in eastern Baltic (Velichko *et al.* 2002)	Chironomid based mean July T °C estimation in eastern Baltic (Kirilova *et al.* 2011)
MA-6 479–497	11340–10960	Boreal forest	Boreal forest	100	–	Younger Dryas/ GS-1	~10.7	~10.7
MA-5 497–534	11340-hiatus	G2 Graminoid forb dwarf shrub tundra	C/D	(5) 50–80	5–9			
MA-4 534–557	hiatus-13545	–	–	–	–	Allerød/ GI-1a–1c	~15.7	
MA-3 557–576	13800–13545	–	–	–	–			~13 13700–12850 cal y BP
MA-2 576–636	13910–13800	G4 Dwarf shrub graminoid tundra	D/E	80–100	7–12			~12 14000–13700 cal y BP
MA-1 636–660	13950–13910	G4/W3 Dwarf shrub graminoid tundra/wetland	D	50–80	7–9			

Table 6d. Lake Lielais Svētiņu plant macrofossil assemblages (MA), possible correlation to modern tundra vegetation zones (CAVM Team 2003), correlation to bioclimatic zones (Walker *et al*. 2005) and different temperature estimations (Walker *et al*. 2005, Velichko *et al*. 2002, Kirilova *et al*. 2011).

MA (depth, cm)	Age, cal y BP	Possible correlation to modern tundra vegetation zones (CAVM Team 2003)	Correlation to bioclimatic zones (Walker *et al*. 2005)	Estimated plant cover % (Walker *et al*. 2005)	July T °C based on bioclimatic zones (Walker *et al*. 2005)	NGRIP events (Lowe *et al*. 2008)	Pollen based mean July T °C estimation in eastern Baltic (Velichko *et al*. 2002)	Chironomid based mean July T °C estimation in eastern Baltic (Kirilova *et al*. 2011)
MA-7 1140–1160	11650–11390	Mixed boreal forest	Mixed boreal forest	100	>10–12	Younger Dryas/ GS-1	~10.7	~10.7
MA-6 1160–1265	12700–11650	G4? Dwarf shrub graminoid tundra to boreal forest	D to boreal forest	50–80/100	7–9; >10 –12			
MA-5 1265–1315	13290–12700	Mixed boreal forest	Mixed boreal forest	100	>10–12	Allerød/ GI-1a–1c	~15,7	~13 13700–12850 cal y BP ~12 14000–13700 cal y BP
MA-4b 1315–1350	13500–13300	Boreal birch forest	Boreal birch forest	100	>10–12			
MA-4a 1350–1405	13760–13500	S2 Low shrub tundra	E	80–100	9–12			
MA-3 1405–1490	14200–13760	G4? Dwarf shrub graminoid tundra	D	50–80	7–9	No data		
MA-2 1490–1515	14400–14200	W2 Sedge dwarf shrub wetland	D	50–80	7–9			
MA-1 1515–1530	14500–14400	–	–	–	–			

determined according to the plant macrofossil records are generally lower than ones estimated for the same time period by pollen and chironomids.
There are different possible explanations for this discordance. The pollen spectra is a reflection of regional floral signal and therefore better characterizing regional climatic trends; plant macrofossils reflect local vegetation and therefore probably also local environmental and climatic conditions. The chironomid record, on the other hand, is a fine-scaled summer temperature proxy with high temporal resolution and temperature error max of 1 °C (Brooks 2007).

This discrepancy between temperature estimations could also be explained by the possible time-lag between large-scale deglaciation and plant species migration from their glacial refugium and furthermore between the migration to regional and local colonization of isolated areas recently freed from ice and water hampering for vegetation development. More warm-demanding species needed time to reach an environment suitable to them by temperature but distant from their initial habitat (f. ex. glacial refugia). Also, the plant macrofossil assemblage from sediment samples reflects only a part of the past floral spectrum, and therefore, some warm-indicative species remains might be not found although it was present.

6.3. Ice recession pattern in the eastern Baltic area

The deglaciation of the southeastern sector of the SIS has been a topic of interest for decades (e.g., Zelčs and Markots 2004, Rinterknecht *et al.* 2006, Raukas 2009). Several deglaciation patterns have been proposed, most of them base on geomorphological features. In the latest review article, Bitinas (2011) analysed glacial landforms and confronted the idea of ice re-advancements, proposing a spatially asynchronous deglaciation with active glacier lobes and dead ice fields. He suggested that the deglaciation of the SIS occurred as surface thinning across a large area rather than as a frontal retreat (*ibid*). The present data collected for thesis support the idea of asynchronous ice lobes, more complex deglaciation, melting of ice across higher elevated areas, and formation of vegetated dry land and lake basins to record it.

The theory in favor of ice front oscillations suggests three major fluctuations during the SIS retreat (Rinterknecht *et al.* 2006). More attention has been paid to its correlation to ice marginal formations (Table 1). The chronologies of the ice recession and deglaciation have been compiled by ^{10}Be datings, varvochronology, radiocarbon dating of “intramorainic” unidentified plant detritus, etc. However, palaeoecology and palaeobotany, besides describing past communities, can also add data to the knowledge on ice recession. Of course, radiocarbon age estimations on terrestrial plant macrofossils do not date the exact moment of deglaciation (or date it indirectly), but the start of sedimentation and the appearance of organic matter and plant remains in the sediments. However, the prerequisites for these processes are deglaciation, the formation of terrestrial ground with enough substance, and favorable environmental conditions to permit vegetation establishment. The time lag between these processes is hard to limit, but today, in suitable conditions, pioneer vegetation will develop within a few years after the glacier retreat. Taking into consideration that the ice recession speed during LG might have been greater than that today (Kalm *et al.* 2011), an observable timing of the vegetation development might contain a migrational time lag.

In recent years, a growing number of palaeoecological studies from localities in the eastern Baltic area have been published with the ^{14}C AMS radiocarbon age estimations (Table 7).

Table 7. Recent studies with AMS radiocarbon dates indicating minimum age estimations for ice margin retreat in the eastern Baltic area.

Selected locations with ^{14}C data	Position relative to ice marginal zones	Start of sedimentation (cal y BP), reference
Tõdva Mire	Palivere	~13 200 (Saarse *et al.* submitted)
Lake Haljala	Pandivere	~13 800 (Saarse *et al.* 2009)
Lake Udriku	Pandivere	~14 000 (Amon and Saarse 2010, Table 4a)
Lake Prossa	Otepää/Pandivere	~14 200 (Kihno *et al.* 2011)
Lake Nakri	Otepää	~14 000 (Amon *et al.* 2011)
Raunis	Haanja (North Lithuanian)	~13 300 (unpublished)
Lake Kuži	North Lithuanian	~12 900 (Koff and Terasmaa 2011)
Solova Bog	Haanja	~14 000 (Amon *et al.* 2010)
Lake Lielais Svētiņu	Middle Lithuanian	~14 500 (Veski *et al.* Paper IV)
Lake Kurjanovas	Middle Lithuanian	>14 700 (Heikkilä *et al.* 2009)
Lake Petrašiunai	Middle Lithuanian	~13 100 (Stančikaitė *et al.* 2009)

The process of deglaciation of Lithuania (review in Guobytė 2004) and the chronology of ice retreatment (Rinterknecht *et al.* 2008) distinguish four ice marginal zones. Their ^{10}Be ages are Grūda moraine (18 300±800 ^{10}Be y BP), Baltija moraine (14 000±400 ^{10}Be y BP), Middle Lithuanian moraine (13 500±600 ^{10}Be y BP), and North Lithuanian moraine (13 300±700 ^{10}Be y BP). The recent radiocarbon age estimations from southern Lithuania show the start of sediment accumulation during GI-1e (Stančikaitė *et al.* 2008). In the northern part of Lithuania, i.e., the Juodonys region, Lake Petrašiunai (Fig. 9) and Lake Rekyva the vegetation development can be dated back to Allerød interstadial (Gaigalas *et al.* 2008, Stančikaitė *et al.* 2004, 2009). There was also an older date from the Juodonys core (14 830–13 680 cal y BP), but it was rejected due to a possible hard-water effect (Stančikaitė *et al.* 2009).

Two localities, Lake Kurjanovas (Fig. 9) and Lake Lielais Svētiņu, are situated in

Figure 9. Scheme of ice lobes and marginal positions of the last Scandinavian Ice Sheet in eastern Baltic area with localitites discussed in thesis. The ice flow scheme is compiled after Karukäpp 2004, Zelčs and Markots 2004 and Kalm 2010. Grey lines and blue arrows depict the main ice flow directions. Orange lines mark probable interlobate zones. Red dotted lines show ice marginal positions. V - Võrtsjärv ice stream; D - Peipsi ice stream; F - Ladoga-Ilmen-Lovat ice stream (Kalm 2010).

eastern Latvia, and geomorphologically, between Middle Lithuanian Moraine and North Lithuanian (Haanja) Moraine (Rinterknecht *et al*. 2006). The deglaciation of the area between the moraines occurred 16 300–14 700 cal y BP (Table 1), based on the datings of ice marginal formations. The age estimations differ significantly with the ice marginal zone location, from 13 500±1000 ^{14}C y BP (~16 300 cal y BP, median) in Lithuania (Rinterknecht *et al.* 2008) to 14 700 cal y BP in Haanja, south Estonia (Kalm *et al.* 2011). It is probably due to the discontinuity of ice marginal zones, the asynchrony of ice recession (Bitinas 2011), and the possible stochastic movements of ice; in some locations the ice retreated, but in another place in the same period, it advanced (Lambeck *et al.* 2010).

Lake Kurjanovas (Heikkilä *et al.* 2009) is located in the Mudava lowland area adjacent to the Latgale upland from the east (Fig. 9). Heikkilä with co-authors suggest that the deglaciation there was more than 16 000 cal y BP in accordance with the estimated ages of nearby ice marginal zone (Rinterknecht *et al.* 2006). However, the time-scale of Lake Kurjanovas is rather tentative, and authors suggest handling the chronology for the lower part of the sediments with caution.

Lake Lielais Svētiņu is situated in the Eastern Latvian glacial lowland (Zelčs and Markots 2004) between the Vidzeme and Latgale glacial uplands. The eastern Latvian lowland was shaped and influenced by the Lubana glacier system that was part of a larger ice stream complex that extended to Western European Russia and Lake Ladoga and entered the Lubana basin from northeast (F^1 ice stream in Kalm 2010). In Lubana, large ice-dammed lakes (Zelčs and Markots 2004) flooded the areas after deglaciation for an unknown period of time. The establishment of terrestrial ice-free ground and the development of vegetation in the surroundings of Lake Lielais Svētiņu in eastern Latvia occurred 14 560 cal y BP in the relatively warm climatic oscillation of LG-termed GI-1e (*sensu* Lowe *et al.* 2008).

The area around Lake Kurjanovas probably deglaciated earlier than the surroundings of Lake Lielais Svētiņu. Lake Kurjanovas is situated somewhat higher than Lake Lielais Svētiņu (111 m.a.s.l. and 96 m.a.s.l., respectively) that probably promoted the earlier deglaciation and neighborhood terrestrialization in regard of the proglacial lake. Therefore, the start of vegetation development as well its preservation in the lake sediments took place earlier east of the Latgale upland than in the eastern Latvian glacial lowland.

The radicarbon dates from the Solova mire in the eastern part of the Haanja heights revealed an age of 14 000 cal y BP (Amon *et al.* 2010). The estimated age for the Haanja stage, southern Estonia, is 15 700–14 700 cal y BP (Kalm *et al.* 2011). The older age (15 700 cal y BP) is estimated based on the age of the Raunis section, Latvia. The much-discussed LG locality Raunis was revisited for new datings in cooperation with scientists from the Latvian University (Fig. 9). The site has been called the most important possible interstadial site in the whole south-eastern Baltic region (Zelčs and Markots 2004, Rinterknecht *et al.* 2006, Bitinas 2011) and the starting point of the LG interval in Estonia (Pirrus and Raukas 1996). The importance of this site is in its "intermorainic" organic layers, therefore presented as probable interstadial sediments (Zelčs and Markots 2004). The previous ^{14}C dates are controversial, showing an age from 13 390±500 ^{14}C y to 10 400±370 ^{14}C y BP (Zelčs and Markots 2004), i.e., from over 16 000 cal y BP to over 12 000 cal y BP. Preboreal age estimations have been acquired from the Raunis outcrop as well (Raukas 2009), although the macrofossil material clearly indicates its LG origin with flora constituents such as *Dryas*, *Salix polaris*, and *Betula nana* (Kalnina *et al.* 2011). The two new AMS ^{14}C dates of the terrestrial macrofossils (abundant wood material) acquired in August 2010 from a 5 m deep test pit in the center of the Raunis basin, where the organic layers are not disturbed by slope processes as in earlier studies, show an age of approximately 13 300–13 200 cal y BP, i.e., the warmest part of Allerød which is in good accordance with the macrofossil finds. The Raunis locality in mid-Latvia, where new dates of around 13 200 cal y BP (Table 4b) were acquired, has to be reinterpreted as that of GI-1c age and not an individual interstadial as considered before (Zelčs and Markots 2004).

The younger age limit for the Haanja stage, 14 700 cal y BP, based on the palaeosecular variation and varvochronology in Lake Tamula (Sandgren *et al.* 1997, Kalm 2006), seems more realistic in the context of the Solova site age estimations. The assessment of the deglaciation age for the area between the North Lithuanian (Haanja) Moraine and the Otepää ice marginal formations is a little vaguer. In the most recent overview, Kalm and co-authors (2011) concluded that ice recession from the Otepää marginal zone occurred “well before” 14 000 cal y BP. It is in accordance with the radiocarbon age estimations from Lake Nakri in south Estonia (~14 050 cal y BP), as by this time the area should have already been deglaciated and suitable for accumulating terrestrial plant remains. The Lake Nakri area was influenced by the Võrtsjärve ice stream (Kalm 2010); in mid-Latvia, other glacial streams developed (Kursian, Usma, and Zemgalian, Zelčs and Markots 2004). The large-scale deglaciation and formation of terrestrial conditions suitable for pioneer vegetation occurred a little later as shown by basal dates from the Raunis and Lake Kuži sections.

Ice recession from the Otepää to Pandivere (Neva) stages should have been completed by 13 800 cal y BP (Saarse *et al.* 2009) to 13 300 cal y BP (Kalm 2006). The last ice marginal formation named on the Estonian territory, Palivere, is calculated to be deglaciated 12 675 cal y BP (Kalm *et al.* 2011). However, the new radiocarbon estimations from the palaeoecological studies listed in this thesis demonstrate remarkably older ages (Table 8).

The LG ice recession chronology, based on the acquired AMS dates of mostly terrestrial plant material, led to unexpected results. The Lake Lielais Svētiņu basal datings confirm the start of organic sedimentation and the presence of vegetation from 14 560 cal y BP (GI-1e). The oldest datings from localities 100 km north, in southern Estonia, Solova, and Nakri, are logically a bit younger, ~14 000 cal y BP. Strikingly, the basal dates from Lake Udriku in northern Estonia are basically from a similar age. Dates from Lake Prossa, in eastern Estonia (Kihno *et al.* 2011), are even older, suggesting the presence of tundra vegetation in that area over 14 200 cal y BP. This contradicts the known ice recession pattern and timescale (Kalm 2006, Kalm *et al.* 2011) calculated from a variety of independent methods.

Table 8. Comparison of ice retreat chronology by Kalm *et al*. (2011) with current minimum age estimations of deglaciation and onset of vegetation colonisation in eastern Baltic area.

Ice marginal zone	Age estimation (cal y BP) of deglaciation *sensu* Kalm *et al*. 2011	Current age estimation (cal y BP) of ice retreat based on new radiocarbon datings of terrestrial plant macrofossils
Palivere	12 700	~13 200 (Saarse *et al*. submitted)
Neva/Pandivere	13 800–13 300	~13 800–14 000 (Saarse *et al*. 2009, Amon and Saarse 2010, Table 4a)
Otepää	>14 000	>14 200 (Kihno *et al*. 2011)
North Lithuanian/Haanja	15 700–14 700	>14 000 (Amon *et al*. 2010)
Middle Lithuanian		>14 500 (Amon *et al*. in preparation)

One possible explanation for this nearly contemporaneous deglaciation in the studied S–N transect lies in the ice flow and hence in its recession pattern. Kalm (2010) differentiates several ice lobes (Võrtsjärve, Peipsi, Ladoga–Ilmen–Lovat, etc.) based on a geoinformatical approach toward the geomorphological features. He also notices the Ladoga–Ilmen–Lovat (F) ice stream as the largest and the most active of all local ice lobes, while the Võrtsjärve (V) and Peipsi (D) ice streams are smaller. One sub-complex of the ice stream F (Lubana complex) affected the LG conditions of the Lubana lowland (Zelčs and Markots 2004), where one of the present study sites, Lake Svētiņu, is also situated. In comparison, the geographically northernmost study locality, Lake Udriku, is one area that was influenced by the V and D ice streams (Fig. 9).

The retreating ice lobes were more active along lowland areas and large depressions such as the Baltic Sea and Lake Peipsi for instance, and the lobes were more inactive along higher areas and possibly a large ice divide line formed. Based on geomorphological data, the theory of different ice lobes of the SIS in eastern Baltic has been proposed before (Fig. 9, Karukäpp 2004, Zelčs and Markots 2004, Kalm 2010) as also the interlobate area in eastern Estonia and Latvia (Karukäpp 2004, Zelčs and Markots 2004). Our results independently confirm the existence of such an ice divide line and separate ice lobes, namely, Võrtsjärve and Peipsi ice lobes on the Estonian territory (Kalm, 2010) and give the time frame for ice lobes recession, which might be earlier than that we know today. Based on radiocarbon chronology, the ice divide line in the Estonian territory opened more than 14 000 cal y BP. That does not rule out that in lowland areas the active ice lobes existed much longer.

7. CONCLUSIONS

The thesis summarizes the postglacial floral establishment and vegetation dynamics in the eastern Baltic area during the LG period 14 500–11 600 cal y BP. Local and regional vegetation development was revealed by plant macrofossils and pollen records from four study localities in the south to north transect from eastern Latvia to northern Estonia. The chosen method, plant macrofossil analysis, proved to be applicable for analyzing LG flora and useful for providing material for AMS ^{14}C datings. The results of plant macrofossil analysis were in good accordance with those provided by other palaeoecological methods, especially the pollen record.

The placement of study locations formed a S–N transect and clearly revealed the time-transgressive and changing nature of the LG environmental conditions in the study area. The vegetation development clearly followed the climatic fluctuations of LG period.

At GI-1e (Bølling) warming, the vegetation development started in eastern Latvia while the rest of eastern Baltic was still unsuitable for vegetation. The analysed palaeobotanical material confirms the northermost Bølling warming evidence so far. The initial pioneer community was scarce but in ~100 years a more productive tundra community emerged. The presence of dwarf birch confirms the minimal summer temperature of 7 °C.

Signs of Older Dryas cooling start at 14 200 cal y BP in eastern Latvia with a decrease both of plant macrofossils and pollen PAR's in the sediments. However, the deglaciation process continued and by the end of GI-1d (~13 900 cal y BP) all the study sites were ice-free and revegetated.

During GI-1c (early Allerød warming) the floral community gradually developped from tundra to birch forest in the southern part of the study area. The minimal summer temperature supporting treeline migration is 10–12 °C. Tree-birch migrated from eastern Latvia to southern Estonia within ~150 years; in North Estonia, treeless tundra conditions prevailed until the Holocene. Pine migrated into the study area (~13 400–13 300 cal y BP), but its distribution is limited to the southern parts of eastern Baltic. GI-1b short cooling did not have major effects on terrestrial plant macrofossil spectra or concentrations.

During GI-1a (post-GI-1b Allerød warming) forest communities dominated in the southern part of eastern Baltic. In eastern Latvia, aspen was introduced to mixed conifer forest community. The favourable climatic conditions supported vegetation development also in North Estonia: the plant macrofossil concentration is rather high and spectra contain a variety of different herbs and shrubs.

Younger Dryas (GS-1) cooling had a remarkable impact to vegetation in the eastern Baltic area. The tree species vanished and treeless tundra or sparse forest-tundra conditions prevailed again in the study area. Spruce (*Picea abies*) was introduced to the forest-tundra community at ~12 400–12 200 cal y BP as revealed by PAR and findings of stomata and different spruce macroremains since 12 000 cal y BP.

The modeled relationship between PAR and plant macrofossil presence in LG sediments was calculated. The results suggest that the given species of plant macrofossil would be present when *Populus tremula* PAR exceeds 50 pollen grains cm^{-2} y^{-1}, *Picea abies* PAR exceeds 400 pollen grains cm^{-2} y^{-1} and *Pinus sylvestris* PAR exceeds 7500 pollen grains cm^{-2} y^{-1}. *Betula* (tree) PAR and plant macroremain relationship modeling was hampered by the scarcity of tree-birch macroremains in one of the sites under comparison. In case of *Dryas octopetala*, no obvious relationship between PAR and plant macrofossil exists and the presence of palaeobotanical material is probably due to local dispersion, transportation and taphonomy. The modeled PAR values should be tested in multiple core records before any further conclusion could be made.

The age estimations of the start of vegetation development acquired from the study locations allow proposing new limits to the deglaciation history of the study area. The Middle Lithuanian Moraine is >14 500 cal y BP old as the east Latvian study location already supported vegetation development by this time. This age estimation is in accordance with other authors. North Lithuanian/Haanja moraine age, based on Solova Bog record, is over 14 000 cal y BP. Otepää ice marginal zone should be older than 14 200 cal y BP based on data from Lake Prossa. Pandivere ice marginal zone age would be ~13 800 cal y BP. The youngest ice marginal zone in the study area, Palivere, is re-evaluated to be older than previously assumed; the estimation of 13 200 cal y BP is based on record from Tõdva mire.

8. ABSTRACT

Palaeoecological reconstruction of Late-glacial vegetation dynamics in the eastern Baltic area: a view based on plant macrofossil analysis

The present study analyses and presents the postglacial floral establishment and vegetation/community dynamics in the eastern Baltic area during the Late-glacial 14 500–11 600 cal y BP. Local and regional vegetation development was revealed by plant macrofossils and pollen records from four study localities in the south to north transect from eastern Latvia to northern Estonia following the direction of the ice margin recession, namely, Lake Lielais Svētiņu in Latvia, Solova Bog, Lake Nakri, and Lake Udriku in Estonia.

The floral development is tightly coupled with not only the hemispheric-scale climate events but also with local conditions (deglaciation, terrestrialization, topography, and soil properties) in the eastern Baltic region during the Late-glacial. The Late-glacial vegetation succession in the newly deglaciated areas starts with the treeless pioneer tundra community that consisted of different shrubs and telmatic plants. The ameliorating climate permitted the introduction of the first trees – tree-birches (*Betula* sect. *Albae*) – and the formation of forested landscapes around 13 500 cal y BP in the investigation area. The exception is the northernmost front of the study area where the treeless tundra community prevailed until Holocene due to periglacial conditions.

In the southern part of the study area, after tree-birch and pine (*Pinus sylvestris*) migrated at 13 400 cal y BP and expanded, the formation of mixed conifer forest with tree-birch and aspen (*Populus tremula*) formed around 13 300–12 700 cal y BP. In the northern locations of the study area, the conifers were absent or present as sparse individuals. The hemispheric cool climate episode (GS-1) had a remarkable effect on vegetation composition. The species spectrum confirms the presence of tundra communities in the northern part of the study area or the open forest-tundra communities in the southern part of the study area. Spruce (*Picea abies*) was introduced to the forest-tundra community at ~12 400–12 200 cal y BP as revealed by pollen accumulation rates and findings of stomata and different spruce macroremains since 12 000 cal y BP. Holocene forest expansion and the introduction of warmth-demanding species occurred at ~11 700–11 600 cal y BP all over the area.

9. KOKKUVÕTE

Hilisjääaegsed taimkatte muutused Ida-Baltikumis taimsete makrojäänuste analüüsi põhjal

Doktoritöö käsitleb Ida-Baltikumi pärastjääaegset taimestumist ning taimkatte arengut hilisjääaegsete kliimamuutuste kontekstis 14 500–11 600 aastat tagasi. Ülevaade põhineb paleoökoloogilisel andmestikul Ida-Lätist Põhja-Eestini, lähtudes mandrijää lõuna-põhjasuunalisest taandumisest. Uuriti nelja hilisjääaja vanusega setteläbilõiget; kompleksne analüüs hõlmas taimsete makrojäänuste ja õietolmu analüüsi, orgaanilise aine sisalduse määramist ning taimsete makrojäänuste dateerimist radiosüsiniku meetodil.

Doktoritöös rakendatud taimsete makrojäänuste analüüs võimaldas taastuletada hilisjääaegset taimkatte arengut, arvukad maismaataimede jäänustest tehtud radiosüsiniku dateeringud lubasid selgitada taimkattes toimunud ajalis-ruumilisi muutusi. Uurimisala taimestumine algas Lätis enam kui 14 500 aastat tagasi, Eestis algas taimestumine hiljem umbes 14 000 aastat tagasi. Esmane taimestik koosnes kõigil uurimisaladel tundrakooslustest, lõunast põhjasuunda olid domineerivateks liikideks vaevakask, drüüas ja polaarpaju. Kliima soojenemine Allerødis võimaldas puude sisserännet Ida-Baltikumi. Kasemets moodustus Lätis 13 500 aastat tagasi, Lõuna-Eestisse jõudsid kasemetsad 150 aastat hiljem, kuid Põhja-Eestisse see liik hilisjääajal ei levinud. Põhja-Eestis domineerisid arktilised tundrakooslused kuni Holotseeni alguseni 11 650 aastat tagasi. Lätis järgnes kasele männi ning ka haava sisseränne ning 13 300–12 700 aastat tagasi domineerisid Ida-Lätis ja Lõuna-Eestis segametsad.

Hilis-Dryase jahenemine 12 850–11 650 aastat tagasi muutis märgatavalt taimkatte koosseisu. Puuliigid taandusid soojema kliimaga aladele ning Ida-Baltikumis levis taas tundrataimestik. Hilis-Dryase teises pooles 12 400 aastat tagasi levis Läti aladele kuusk, selle liigi sisserände kohta Eestisse antud uurimus kinnitust ei leidnud. Holotseeni alguses 11 650 aastat tagasi muutus kliima soojemaks, millega kaasnes Ida-Baltikumi ala kiire metsastumine ja lehtpuude laialdasem levik.

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PAPER I

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Late glacial multiproxy evidence of vegetation development and environmental change at Solova, southeastern Estonia

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Abstract. Reinvestigation of the late glacial Solova (Remmeski) basin, based on plant macrofossil and diatom record, AMS ^{14}C chronology and sediment composition (loss-on-ignition and magnetic susceptibility data), provided information on vegetation history and palaeoenvironmental and palaeoclimatic changes since the time of the deglaciation of the area around 14 000 cal yr BP. The chronology of the sequence is based on seven AMS dates on terrestrial macrofossils, providing evidence of rapid sedimentation in between 14 000 and 13 500 cal yr BP. Loss-on-ignition data show a clear short-lived warming episode centred to 13 800 cal yr BP, tentatively correlated with the GI-1c warming of the event stratigraphy of the Last Termination in the North Atlantic region, which suggests that at least parts of the Haanja Heights were ice-free by 14 000 cal yr BP. Macrofossil evidence indicates *Betula nana–Dryas octopetala*-dominated open tundra communities with *Saxifraga* on dry ground, and *Carex* sp. and *Juncus* on wet ground at that time. The first evidence of the postglacial presence of tree birch (*Betula pendula*) in Estonia is dated back to 13 500 cal yr BP. However, conifer remains were not found in the late glacial sediment sequence of Solova Bog. The late-Allerød (GI-1a) organic deposits, which are quite typical of other parts of Estonia and indicate general warming, are missing at Solova, most probably due to a hiatus in sedimentation in this very small and shallow upland basin.

Key words: plant macrofossils, aquatic macrophytes, diatoms, geochronology, late glacial, deglaciation, Estonia.

INTRODUCTION

The Late Weichselian deglaciation and the following vegetation formation and succession pattern in the eastern Baltic area have been a topic of interest since Hausen (1913), who initially outlined the ice-marginal positions of the last glaciation in Estonia. The ice-shed line (Karukäpp 2004) amid the glacier flows of the Gulf of Riga (Baltic ice stream complex) and Lake Peipsi–Pskov, starting between the junction of Salpausselkä end moraine arcs in the north (Lundqvist 1987) and running along the Pandivere Upland, and the Otepää and Haanja Heights and the Latgale Upland consecutively in the south, delimits a narrow NW–SE-trending area of a possibly thinner and inactive glacier that may have been more vulnerable to the Bølling–Allerød warming (GI-1; Lowe et al. 2008) between 14 700 and 12 858 cal yr BP. Thus, the southeasternmost part of Estonian territory was probably liberated from ice first, however, the exact time is still poorly known. In addition, this ice-divide might have served as a primary passage for migrating late glacial vegetation.

The aim of this study is to shed light on the much-debated chronology of the onset of deglaciation in the southernmost part of Estonia (e.g. Raukas et al. 2004; Kalm 2006; Rinterknecht et al. 2006). Additionally, we hope to clarify the local vegetation development after the retreat of ice, which, in turn, may indicate climate change in late glacial time. Fossil plant macrofossils have proven to be an exceptionally reliable tool for reconstructing past local vegetation cover in recently deglaciated areas (Birks 2003). Moreover, the dating of carefully selected terrestrial plant macroremains contributes to the accurate deglaciation chronology. Because of its geographical position at the southern border of Estonia, topographically rather high (168 m a.s.l.) on the Haanja Heights in the ice-shed zone, Solova is probably one of the oldest postglacial sedimentary basins on the current territory of Estonia, which has yielded evidence of late glacial warming. Results of the palaeobotanical study at the Solova site reflect traces of the first vegetation succession and postglacial tree limit dynamics in Estonia after the Last Glacial Maximum (LGM), giving therefore valuable information not only about a local-scale palaeoenvironment, but also about palaeoclimatological shifts in a regional scale. Present results, combined with recent palaeoecological and chronological data from the neighbouring areas (e.g. Stančikaitė et al. 2008; Amon et al. 2009; Heikkilä et al. 2009; Saarse et al. 2009; Amon & Saarse 2010), will contribute to our knowledge about deglaciation of the eastern Baltic area and ice sheet decay in the southeastern sector of the Scandinavian Ice Sheet, as well as about the vegetation succession pattern and timing in these areas.

STUDY SITE

Solova Bog (Fig. 1; 57°42.024′ N; 27°24.915′ E) is located in the eastern part of the Haanja Heights (Viitka–Luhamaa hummocky area) at the Estonian–Russian border at an elevation of 168 m a.s.l. The surroundings of the bog reach in places ca 230 m a.s.l. Solova Bog is today a drained and forested wetland some 12 ha in size, however, the basin area containing late glacial deposits is limited only to 75 m in diameter on the Estonian side.

The Solova site, formerly known as Remmeski, is a well-known late glacial reference site for the Estonian stratigraphic scheme (Pirrus & Raukas 1996). There is some confusion, though, in the earlier data as Solova (12 ha) and Remmeski (118 ha) bogs lie just 5 km apart. The majority of investigations seem to have been conducted at the Solova site but published under the name of Remmeski Bog, and some studies from the Remmeski site under its proper name. Pollen evidence from the 'real' Remmeski Bog was first published by Veber et al. (1961) in the frame of investigations of peatland-type sections of upland areas. Pirrus (1969) investigated the late glacial pollen composition of the Solova sequence and speculated on the 'older than Allerød' pollen spectra, represented as elevated pine pollen percentages below 'typical Allerød' strata (R. Pirrus pers. comm. 1996), and included the site in the stratigraphical scheme of the Estonian late glacial (Pirrus & Raukas 1996). Unfortunately Pirrus (1969)

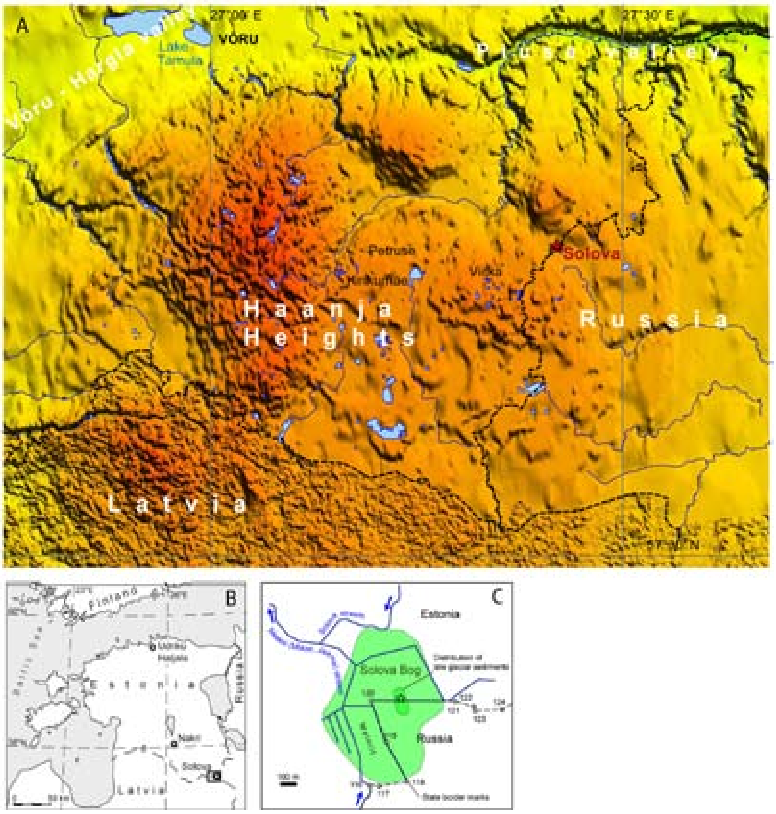

Fig. 1. (A) Location of Solova Bog (marked with a star) in the eastern part of the Haanja Heights elevation model on the border between Estonia and Russia. Location of sites in the vicinity of Solova is marked. (B) Location of the investigated area in southeastern Estonia. (C) The immediate surroundings of Solova Bog.

mixed up the site names and published her results under the name of Remmeski. Radiocarbon dates under the name of Remmeski are available both from the late glacial and Holocene sediment layers (Punning et al. 1971) and have yielded ages around 12 750 ± 145 cal yr BP for the late glacial part, yet, it is unclear whether these ^{14}C-dated samples were taken from the Solova or Remmeski site. Despite the confusion with the locality names, the Solova basin remains an important late glacial key site to which we now try to implement AMS ^{14}C chronology based on terrestrial macrofossils and determine local vegetation development based on plant macrofossil evidence.

METHODS

In August 2007 a sediment core was taken for AMS ^{14}C chronology from Solova Bog, using a Russian peat sampler 10 cm in diameter and 1 m long. Sediments down to the sand layer at the bottom were recovered, a maximum sediment thickness of 670 cm was recorded and sediment lithostratigraphy was described. The cores were photographed, carefully packed into 1 m plastic semitubes, wrapped in polyethylene film, labelled and transported to the laboratory. An additional set of replicate cores for macrofossil analysis was taken from exactly the same place as the previous coring point in September 2008.

The chronology of the sediments was established using seven AMS radiocarbon dates on terrestrial plant macrofossils. The radiocarbon dates were converted to calibrated median ages using the IntCal04 calibration dataset (Reimer et al. 2004) and the OxCal 4.0 program (Bronk Ramsey 2001). All ages mentioned in the text refer to calendar years before present (cal yr BP; 0 = AD 1950).

The organic matter (OM) content was measured as loss on ignition after heating dried samples at 550 °C for 4 h (Heiri et al. 2001). Magnetic susceptibility (MS) was measured from the whole length of the core on the sediment surface at 1 cm resolution using a Bartington Instruments Ltd. high-resolution surface scanning sensor MS2E. Measurements were performed from the cleaned sediment surface covered with a thin plastic film. Results of MS values are expressed in SI units.

Plant macrofossil analysis was carried out in contiguous 4 cm intervals from the sediment core at depths between 660 and 480 cm. The uniform subsample size (approximately 300 cm^3) was determined by displacement of water in a measuring cylinder. The preparation for plant macrofossil analysis followed conventional procedures (Birks 2001). Material retained on sieves was examined using stereo- and light microscopes. The material identified was mostly plant macrofossils (seeds, catkin scales, endocarps, etc.) but also remains of different aquatic animals and moss fragments. Moss analysis was performed for the core depth interval 657–557 cm. Several specimens were identified to genus level due to poor preservation or identification problems. The group *Drepanocladus sensu lato* sums up different *Drepanocladus* and *Warnstorfia* species. *Sphagnum* was also united into one group due to lack or detachment of stem leaves. Plant macrofossil and moss atlases (e.g. Aalto 1970; Abramov & Volkova 1998; Ingerpuu & Vellak 1998; Cappers et al. 2006) were used for identification. In addition, seed collections and herbaria of the Department of Environmental Archaeology, National Museum of Denmark, and W. Szafer Institute of Botany, Polish Academy of Sciences, were employed. The moss nomenclature follows that of Ingerpuu & Vellak (1998). Plant macrofossil zonation follows constrained incremental sum of squares (CONISS) cluster analysis (Grimm 2007).

For diatom analysis freeze-dried sediment was weighed and the samples were digested in 30% H_2O_2 until organic material was oxidized. A few drops of 10% HCl were added to remove carbonates and thereafter the fine mineral particles were removed by repeated decantation. Commercially available divinylbenzene microscopic markers were added to determine diatom concentration. A few drops of the cleaned subsample were dried onto the cover glass and mounted on slides using Naphrax medium and analysed for microfossils under a Zeiss Imager microscope at × 1000 magnification, using oil immersion and differential interference contrast optics.

RESULTS

Lithostratigraphy and chronology

Only the lower part of the sediment core, from 670 to 480 cm, was studied. Details of the sediment lithostratigraphy are presented in Table 1. The basal part of the section consists of 180 cm thick minerogenic sediments that are overlain by gyttja and peat deposits. Coarse-grained clastic sediments, namely medium and fine-grained sands, which constitute the lowermost sediments of the sequence, have overall low OM values. The MS values are very low at the base of the core but increase notably further up in the sequence. These sediments are interpreted as having accumulated immediately after the deglaciation. A distinct shift in the sediment grain size and MS values occurs at a depth of 560 cm. Above the 487 cm level, minerogenic sediments are overlain by OM-rich lacustrine gyttja sediments.

The chronology of the core is based on seven AMS dates on terrestrial macrofossils (Fig. 2A). An age/depth plot shows that the lower part of the sediment section

Table 1. Lithostratigraphic description of the sediment sequence at the Solova site

Depth from the surface, cm	Sediment description
450–487	Gyttja, homogeneous, olive to green; OM = 17–82%; MS = 0–1 (× 10^{-5}) SI
487–516	Silt with diffuse organic matter and plant fragments; light greenish-grey, distinctly darker more organic-rich layers at 493–495, 498–502 and 508–512 cm; OM = 4.0–12.6%; MS = 0–6 (× 10^{-5}) SI
516–560	Clayey silt/silty clay, grey; OM = 2.3–4.0%; MS = 3–11 (× 10^{-5}) SI
560–624	Silt, beige; OM = 2.1–2.9%; MS = 12–28 (× 10^{-5}) SI
624–637	Clayey silt, massive, light beige; OM = 3.4–5.6%; MS = 24–35 (× 10^{-5}) SI
637–666	Silt with sandy interlayers, laminated, grey; OM = 1.7–2.8%; MS = 18–30 (× 10^{-5}) SI
666–672	Sand, medium to fine-grained, brownish-grey; OM = 0.7–2.1%; MS = 3–19 (× 10^{-5}) SI

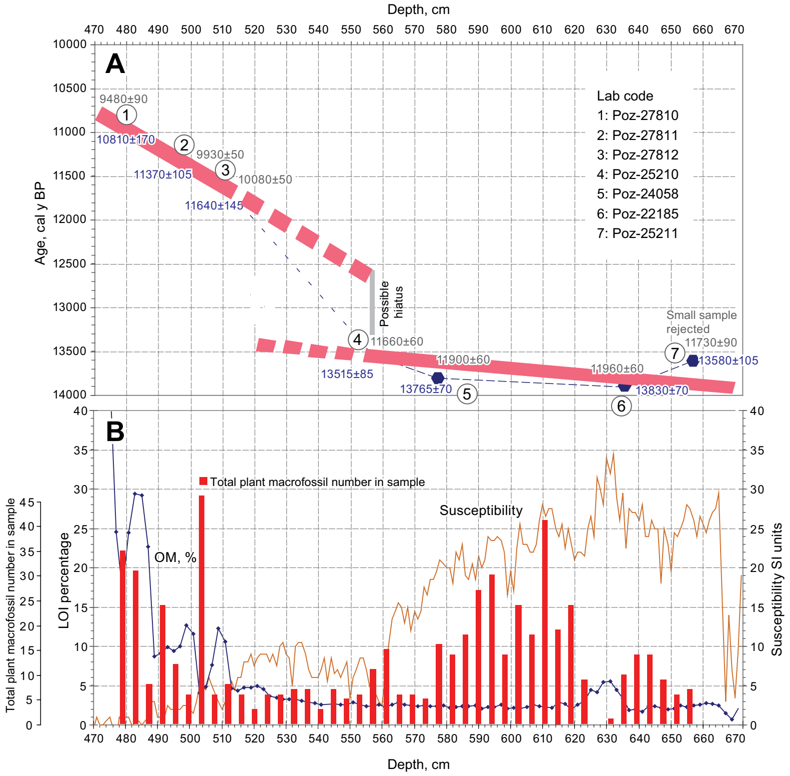

Fig. 2. (A) The age–depth model of late glacial sediments of Solova Bog with the possible hiatus indicated. Chronology is based on ^{14}C dates and calibrated ages BP (median age with 2 σ error margins). The bottommost sample No. 7 was rejected from the age–depth model due to unexpected results from a very small sample (less than 0.2 µg C). (B) Graph showing LOI percentages (solid line with diamond markers), magnetic susceptibility in 10^{-5} SI units (solid line) and total plant macrofossil number (bars) along the depth scale.

(core depth 630–560 cm) deposited around 13 800–13 500 cal yr BP and suggests a high sedimentation rate (over 0.2 cm/yr). The lowermost AMS ^{14}C date produced a 'younger than expected' age, possibly due to a very small quantity of dated material and was rejected. The dating at a depth of 512 cm yielded an age of 11 640 ± 145 cal yr BP, i.e. the Pleistocene–Holocene boundary. The other dates from the upper portion of the core were consistent and suggested a uniform but apparently slower sedimentation rate compared to the lower portion of the core. The age/depth curve implies a possible hiatus in the sediment record (Fig. 2). Considering the distinct change in lithostratigraphic parameters, the hiatus could be located at a depth of 560 cm, on the boundary between silt and clay sediments. In that case a gap of about 1000 years in sedimentation persists, i.e. between ca 13 500 and ca 12 500 cal yr BP, suggesting that the climatic events of the Last Termination GI-1a and GI-b and the initial part of GS-1 (Lowe et al. 2008) are partly absent from the Solova sediment record.

Plant macrofossils

The macrofossil record of the Solova basin is divided into six macrofossil assemblage zones (SMZ) in accordance with CONISS cluster analyses. Results of the macrofossil concentrations are given in Fig. 3.

In the lowermost zone (SMZ-1, 660–636 cm, fine-grained sand/silt) the abundance of plant macrofossils is low; only few scattered remains of arctic plant taxa are present. In SMZ-2 (636–576 cm, clayey silt) the majority of taxa are similar to those in SMZ-1; however, the abundance of macrofossils increases up to 40 finds per sample. The finds are mainly leaves of *Dryas* sp., but in addition, the remains of *Betula nana*, *Juncus* and *Potamogeton filiformis* are noted.

In SMZ-3 (576–557 cm, clayey silt/silt) the abundance and richness of plant species declines compared to the previous zone. In SMZ-4 (557–534 cm, silty clay/silt) macroremains of *Juncus* disappear and the number of *Daphnia* ephippia increases. At the lower boundary of the zone a remain of *Betula pendula* was recorded. Around the core depth of 530 cm, in SMZ-5 (534–497 cm, silt with plant fragments), a clear shift in macroremain composition is observed (Fig. 3). Arctic species such as *Dryas octopetala* and *Betula nana* almost disappear above this level and the macrofossil assemblage is dominated by aquatic and telmatic plant remains (Potamogetonaceae, *Ranunculus* sect. *Batrachium*). The abundance of Characeae oospores increases simultaneously. The uppermost zone SMZ-6 (497–479 cm, silt with plant material/gyttja) contains macroremains of tree-birch, *Alnus* and *Phragmites*, and suggests a shift in the vegetation towards an assemblage of a much warmer climate. Moreover, in SMZ-6 the burst of limnic animal remains occurs – hundreds of *Daphnia* ephippia and *Cristatella mucedo* statoblasts were identified.

Diatoms

Most of the lower part of the studied sediment sequence was devoid of diatoms (Fig. 4). This can be ascribed to a high accumulation rate of mineral particles, possibly causing considerable dispersion of diatoms. Diatom scarcity can also be attributed to poor preservation through dissolution of diatom frustules. From a core depth of 500 cm benthic diatoms appear, notably small-sized fragilarioid diatoms. From a depth of 485 cm, the diatom composition becomes more diverse. The first planktonic diatoms (e.g. *Cyclotella comensis* and *C. comta*) appear, *Fragilaria* species decline and are replaced by epipelic taxa such as *Navicula radiosa* and *N. diluviana*, as well as by epiphytic/epipsammic *Achnanthes minutissima*.

DISCUSSION

The development of terrestrial environment at Solova

The terrestrial vegetation record at Solova begins at approximately 14 000 cal yr BP (Fig. 3). Correlation of the studied time interval with the ice core data suggests that the lower portion of the sedimentary record at Solova (660–557 cm) can be associated with the GI-1c event (Lowe et al. 2008), a 650-year-long slightly warmer episode of the late glacial period. Species richness in the lowermost part of the sediment core is low. The main species found, *Betula nana* and *Dryas octopetala*, are typical pioneer plant species of the late glacial period, which provide information about the local terrestrial biota, suggesting rather severe climate conditions up to 13 500 cal yr BP (660–556 cm). In addition, *Juncus* and *Carex* remains indicate wet surroundings of the locality. Between core depths of 635 and 627 cm around 13 800 cal yr BP adjacent samples are practically empty of plant macrofossils, except for one grass seed. This coincides with a slight rise in the OM content of sediment (Fig. 2). High MS values at the same level are likely indicative of catchment erosion and fast material (including paramagnetic particles) inwash into the basin, possibly supplemented with higher soil organics input, rather than increased autochthonous organic production, which otherwise would seem to be the most likely explanation for higher OM content. Lack of plant macrofossils in this small section may be related to local amelioration shown by more organic-

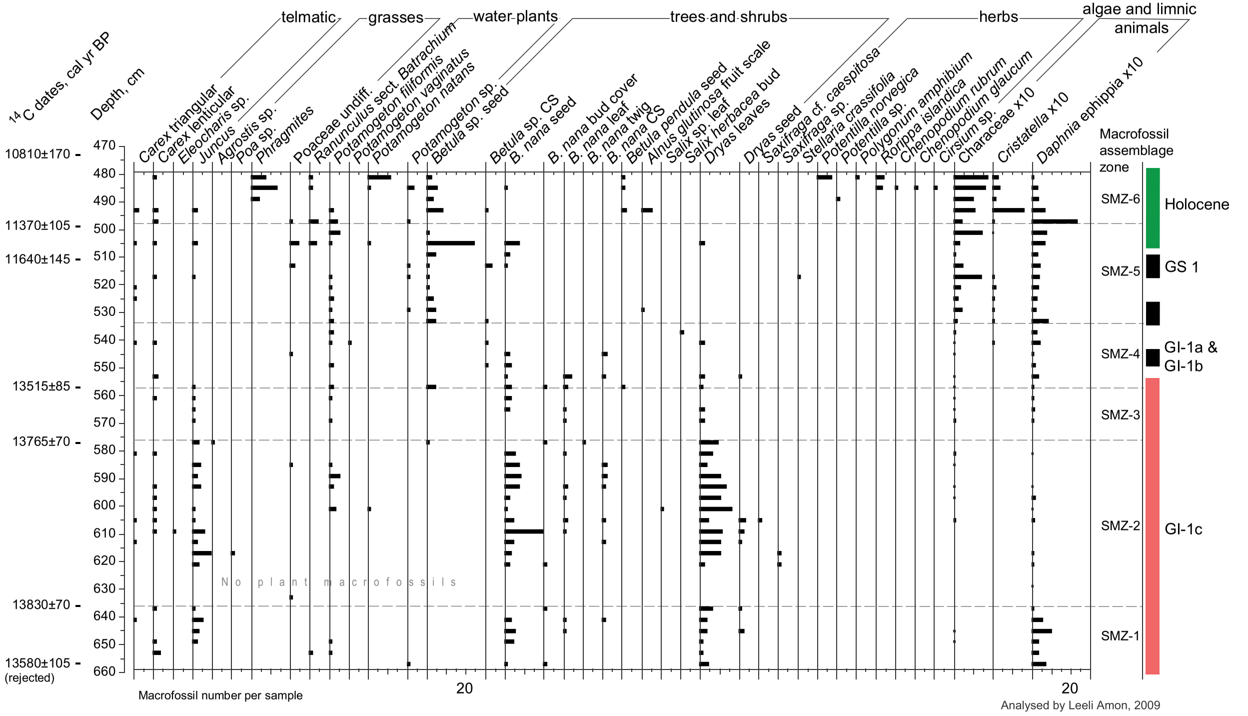

Fig. 3. Macrofossil diagram for Solova Bog (number of specimens per sample) plotted against age (cal yr BP) and correlated with schematic Greenland ice core chronology (Lowe et al. 2008). CS, catkin scale.

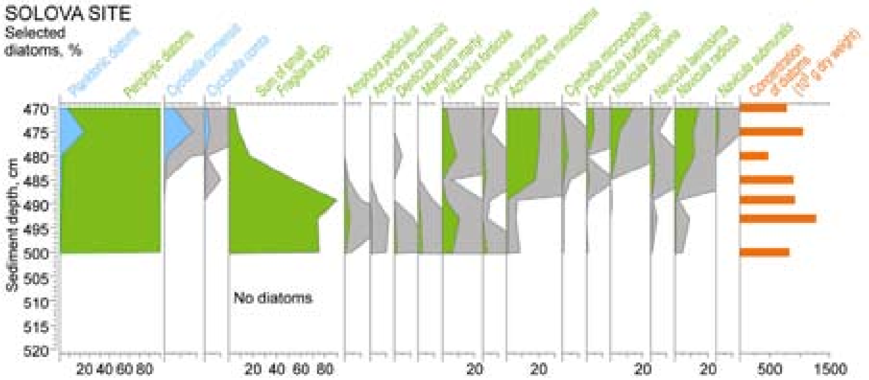

Fig. 4. Diatom stratigraphy of the main taxa as relative abundance (%), proportion of plankton and periphyton (%) and diatom concentration (10^5 g dry weight) from the Solova Bog sediment sequence. The grey curves show 10 × exaggeration of the percentage values.

rich sediments, but the deterioration of preservation conditions does not allow us to draw further conclusions about local vegetation development, based on indicators of terrestrial environment. After ca 13 800 cal yr BP the terrestrial vegetation reflected by plant macrofossils consists of arctic species and suggests open tundra landscape, proved by the presence of light-demanding species like *Dryas* and *Saxifraga*. Remains of telmatic species such as *Juncus*, *Eleocharis* and *Carex* are indicative of wetland around the lake. From ca 13 750 cal yr BP the abundance of plant macroremains falls considerably but the species composition is more or less the same, i.e. *Betula nana*, *Dryas* leaves and *Juncus* seeds. The first macroremain find of the real tree-birch *Betula pendula* from the Solova sediments (559–555 cm) may refer to a short-time climate warming at 13 500 cal yr BP, just before the suggested hiatus. However, from this point onwards the use of the exact temporal scale is hampered by a possible sedimentary hiatus (Fig. 2).

The total plant macrofossil concentration is the lowest at the 556–510 cm level (Fig. 2), suggesting colder Younger Dryas conditions. A distinct rise in the abundance of plant macrofossils occurs at a depth of 510 cm at the Younger Dryas–Preboreal boundary. A series of samples consist of *Betula* sp. seeds – wingless or decayed birch seeds. These seeds could be either dwarf or tree birch seeds.

The transition to the Holocene at ca 11 650 cal yr BP (Lowe et al. 2008) is revealed by a principal change in plant species composition. Both, tree species (*Betula pendula*, *Alnus glutinosa*) and herbs are reflecting ameliorated environmental conditions. In the section analysed the variety of herbs is the largest in the early Holocene. The presence of *Phragmites* suggests the proximity of wetland, as does the occurrence of *Carex*, *Juncus* and *Polygonum amphibium* seeds. On the other hand, the terrestrial herb community enlists *Potentilla norvegica*, which nowadays is largely present in sandy and gravelly grounds all over the Scandinavian Peninsula. *Rorippa islandica* is indicative of wetter clayey ground, showing as well unstable open surfaces around the sampling site.

The development of aquatic environment

The initial assemblage of aquatic organisms in the Solova basin at ca 14 000 cal yr BP consisted of two plant species, *Potamogeton filiformis* and *Ranunculus* sect. *Batrachium*. Both are cold-tolerant species, usually associated with relatively turbid waters, and are likely to imply an intensive mineral soil inwash from the catchment (Väliranta 2006). *Daphnia* ephippia were present at the start of postglacial sedimentation. *Daphnia* spp. often colonized newly created water bodies (Sarmaja-Korjonen 2003; Sarmaja-Korjonen et al. 2006), e.g., they were the first immigrants in the late glacial Lake Kråkenes in western Norway (Birks 2000). In Solova, 13 800 cal yr BP, however, the amount of aquatic remains declined, except for a small cluster of *Potamogeton filiformis* endocarps and the appearance of a cosmopolitic pondweed species, *Potamogeton natans*. The shortage of limnic macroremains around a core depth of 630 cm rather suggests an event of rapid inwash of autochthonous OM and considerable minerogenic contribution (high MS values) to sediment matrix, which caused a pronounced dilution effect of fossil remains. Alternatively, a harsh climate with long-lasting ice cover, when only a narrow marginal belt of open water existed in the lake during the short summer season, precluded the development of the aquatic biota populations in the basin.

From approximately 13 600 cal yr BP (570 cm), the occurrence of *P. filiformis* endocarps in the samples is almost continuous albeit in small numbers. From the same time onwards, also *Daphnia* remains are constantly present in sediment and show a rising trend.

The only find of *Potamogeton* cf. *vaginatus*, a nowadays rare Nordic pondweed species that prefers deep brackish-water conditions, comes from 540 cm depth (suggested age around 12 300 cal yr BP). At the same time *Cristatella mucedo* statoblasts appear in the sediment record and the abundance of Characeae oospores rises considerably. This change in the community of water organisms precedes the rising trend in the concentration of terrestrial macrofossil remains. A similar pattern – the increased abundance of algae, although microscopic ones, followed by higher concentrations of plant remains – is observed at the Pleistocene–Holocene boundary at Nakri (Amon et al. 2009). Above the 530 cm level (around 12 000 cal yr BP) oospores are present in all samples, numbering between 4 and 160 per sample. However, the counts of oospores are relatively small compared to other studies where thousands of Characeae oospores were recovered in smaller sample volumes (e.g. Birks 2000), suggesting a limited amount of fructifying algae in the given conditions.

Temporarily, during the end of the Younger Dryas or the onset of the Holocene, *Ranunculus* sect. *Batrachium* reappears, indicating rise in water temperature (Birks 2000). The population of limnic organisms and Characeae is rich also in the Holocene part of the studied section. Temperature-sensitive *Cristatella mucedo* (Økland & Økland 2000) displays a maximum at 11 300 cal yr BP (490 cm), confirming mild conditions in water environment at that time.

Small-sized *Fragilaria* spp. are often associated with high environmental instability. They reproduce quickly and tolerate shorter environmental oscillations, which makes them very competitive in unstable limnological conditions (e.g. Haworth 1976; Korhola & Weckström 2004). Thus, the peak of the pioneer forms of *Fragilaria* spp. in the Solova sediment profile may temporarily be linked with the onset of Holocene rapid climatic change (Fig. 4).

The appearance and increase of planktonic diatoms, namely *Cyclotella* spp. (485 cm), in the sediment record may be related to milder and stabilized climate in the Early Holocene. During warmer years the ice cover is less extensive, and hence the growing season is lengthened and planktonic diatoms may be relatively more abundant. Marked increase in the abundance of planktonic diatom assemblages is apparent in the 150-year-long palaeoclimate record from northern Lapland lakes, reflecting recent climatic warming (Sorvari & Korhola 1998). However, the overall diatom composition and dominance of littoral diatoms indicate a very shallow hard-water lake for the Solova basin.

Mosses

Only a few studies of moss fragments as a possible palaeoecological proxy are available from Scandinavia (e.g. Bennike & Hedenäs 1995; Jonsgard & Birks 1995) and a few from Estonia, whereas the latter deal mostly with *Sphagnum* species and mires/wetlands (e.g. Sillasoo et al. 2007). However, the richness of moss species and well-characterized recent ecological amplitude should encourage the use of moss analysis for (late glacial) palaeoenvironmental studies (Janssens 1990). Only a limited number of bryophyte species were identified from the sediments of Solova Bog. The presence and absence of species is presented on the stratigraphic scale in Fig. 5.

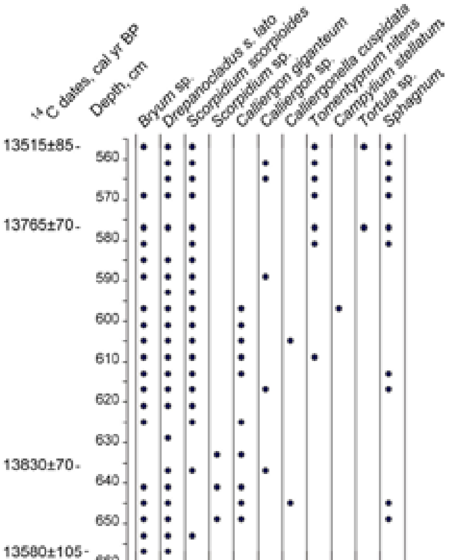

Fig. 5. Moss species presence/absence in the lower section of the sediment core from Solova Bog.

Moss fragments identified (from 657–557 cm) are represented mostly by widespread aquatic mosses in the lower part of the sediment section, with a succession of fen and even more terrestrial species upwards in the core. *Scorpidium scorpioides* is present throughout the section; this species has also been found since the Saalian period in Denmark (Odgaard 1981). *Calliergon giganteum* was identified in the lower half of the analysed sediment sequence. Today *C. giganteum* is a circumpolar moss species that prefers water-rich environment (Koponen et al. 1995). *Tomentypnum nitens* appears first in the middle of the section and is constantly present in the upper part of the sequence. *Tomentypnum nitens* is found also in the earliest Holocene sediments of Svalbard and is interpreted as a species occurring in mineral-rich or calcareous wetland habitats (Bennike & Hedenäs 1995). Another fen-indicative species is *Campylium stellatum*, the only occurrence of which is in the middle of the sediment core (approximately 13 850 cal yr BP). The presence of *Tortula* in the upper part of the sequence clearly shows the proximity of a shore or a higher ground as all recent species from this genus that grow in Estonia prefer terrestrial and even dry habitats.

Pollen evidence of environmental change

The majority of lakes and bogs on the Haanja Heights are relatively young, formed predominantly in the Preboreal (e.g. Punning et al. 1995; Niinemets & Saarse 2006) due to glaciokarstic processes. Only in a few of them, such as Lake Kirikumäe and Solova (Remmeski) Bog, postglacial sediments started to accumulate in the late glacial period (Pirrus 1969; Saarse & Rajamäe 1997).

The Solova sediment core has been studied for pollen content (Pirrus 1969; Sarv 1983) and is considered as one of the type sections for Estonian late glacial stratigraphy (Pirrus & Raukas 1996). Solova pollen spectra represent typical late glacial vegetation composition comprising grasses, sedges and dwarf birch, however, a specific section with a high percentage of tree pollen occurs below layers of the Younger Dryas flora. This feature – high amounts (over 80%) of pine pollen, is characteristic of the Allerød in earlier published pollen stratigraphies of Estonian late glacial sediments, which we in the light of recent data from the adjacent area (Amon et al. 2009) can attribute to the latest part of the Allerød (GI-1a). Unfortunately, there were no valid radiocarbon ages tied to pollen stratigraphy and therefore it is questionable to correlate recent macrofossil data and the pollen diagram of Pirrus (1969).

Features of vegetation development similar to that at Solova are seen in the Lake Kirikumäe pollen record from the late glacial period (Saarse & Rajamäe 1997). The oldest radiocarbon dates from Lake Kirikumäe are from the Preboreal, but pollen data extend into the late glacial so-called Allerød (GI-1a or GI-1b according to Lowe et al. 2008), indicating that a certain area in the eastern Haanja Heights has been ice-free since 14 000 cal yr BP, i.e. after the Older Dryas.

Reconstruction of terrestrial vegetation cover in southeastern Estonia

Tree species migration and tree line dynamics in the late glacial period (Willis & van Andel 2004; Kullman 2008) and in the Holocene (e.g. Giesecke & Bennett 2004) have deserved attention in modern palaeoecology due to their relationship with the contemporary climatic and environmental conditions. In areas affected by the ice front recession of the LGM, climate ameliorations/deteriorations are important factors for re-introduction of species into the local environment. In respective studies plant macrofossil data, although with similar limitations, may be more favourable than pollen evidence due to low pollen productivity in lower temperature conditions and possible resedimentation of pollen from earlier time periods. Pollen spectra from closely spaced sites (Solova and Lake Kirikumäe) indicate high pollen percentages for trees (birch, 60%) in the early late glacial. Macrofossil evidence, though, implies no tree cover at Solova at that time. We do not have chronological control over pollen evidence at Solova, but we argue that the pre-Allerød higher tree pollen values show non-local production and may coincide with the higher OM content at 13 800 cal yr BP at Solova (Fig. 2), thus suggesting the reflection of the GI-1c warm episode in the recently ice-freed environment of SE Estonia. The herb/shrub composition (*Artemisia*, Chenopodiaceae, grasses and sedges) in pollen evidence of the same time differs/complements the macrofossil data displaying a grass–sedge–shrub tundra community.

At the Solova site macrofossils of mostly shrubs are found, the most common of them being dwarf birch (*Betula nana*), which is present throughout the late glacial to the Holocene. *Betula nana* is also commonly mentioned in other studies of late glacial sediments of the region (e.g. Wohlfarth et al. 2002) and has been reported to have grown near the ice margin even during the LGM (Binney et al. 2009). *Salix* remains at Solova occurred in small quantities; however, willows (probably of shrub growth forms) are not rare in the Estonian late glacial vegetation, as shown by evidence from the Udriku (Amon & Saarse 2010) and Nakri (Amon et al. 2009) localities. Different *Salix* species have also been recognized in various regions in Eurasia from before the LGM to the present (Binney et al. 2009).

Tree-birch species, of which *Betula pendula* was identified in Solova sediments, are more indicative of climate warming. The first occurrence of the tree-birch is approximately 13 500 cal yr BP. At the adjacent (70 km N) Nakri site (Amon et al. 2009) the first occurrence of the tree-birch was dated around 13 400 cal yr BP, that is ca 100 years later than in Solova. In modern Fennoscandia birch forms the forest–tundra transition zone (Hustich 1983) and it seems to be the case in the eastern Baltic late glacial as well.

It is noteworthy that only 130 km to the southeast of Solova, at Lake Kurjanovas in eastern Latvia (Heikkilä et al. 2009), the onset of forest and its composition were largely different. Logically, the southern regions further away from the ice edge became forested earlier: the closure of the *Pinus* forest at 14 000 cal yr BP is proposed as the first pine macrofossils date from that time. The southern boundary of the present circumpolar Arctic climatic zone is the northern extent of the closed boreal forests. There is no clear boreal forest boundary but a transition from south to north represented by the following sequence: closed forest → forest with patches of tundra → tundra with patches of forest → tundra (Callaghan et al. 2004). The described transition zone is relatively narrow (30–150 km) and quite comparable with the late glacial situation. Tree-birch seeds were found in Lake Kurjanovas sediments, followed by spruce macrofossil around 13 000 cal yr BP, indicating closed forest conditions just 130 km southeast of Solova (Heikkilä et al. 2009). Even further south, in Lithuania, conifer macrofossils were described from the transition from the Younger Dryas to the Holocene (Stančikaite et al. 2008). In principle, spruce may have survived cold episodes of the late glacial period in the northern refugia, as indicated by spruce megafossils in the Scandes Mountains, dated to ca 12 900 cal yr BP and pine dated to 13 500 cal yr BP, i.e. the Allerød warm period (Kullman 2008). In the eastern Baltic area nunatak refugia are hard to imagine and spruce as a continental species (Giesecke et al. 2008) most probably overglaciated somewhere in Belarus (Giesecke & Bennett 2004). East of Estonia, in Karelia, conifers were indicated by pollen only in the Preboreal period (Wohlfarth et al. 2002). Neither at Solova nor at Nakri the macrofossil assemblages (L. Amon et al., unpublished data) did contain conifer remains; even tree-birch remains were scarce, suggesting a rather distinct late glacial forest line somewhere in northern Latvia. The only trace of conifers so far discovered from Estonian late glacial deposits is a few pine stomata (dated back to ca 13 300 cal yr BP) from Lake Nakri, suggesting only rare pine trees in the area.

Deglaciation history

Quaternary glaciations and their geomorphologic features have been studied in many aspects in Estonia (Raukas et al. 2004). Classically, five ice-marginal zones have been distinguished. There are several age estimations from mineral samples (using thermoluminescence, optically stimulated luminescence and cosmogenic ^{10}Be methods) as well from OM (^{14}C datings) and clay varve chronology (Hang 2003; Kalm 2006; Rinterknecht et al. 2006). According to interpretation of pollen diagrams, the retreat of the ice margin from the Haanja zone began in the Bølling period and the area of Estonia was finally ice-free in the second half of the Allerød chronozone (Pirrus & Raukas 1996). The age of the Haanja stage is based on controversial age estimations from the Raunis locality in north-central Latvia (Zelčs & Markots 2004). Radiocarbon age estimations from several sites near Solova, such as Viitka intertill organic layer (Fig. 1) dated to 12 925 ± 65 and 13 020 ± 100 cal yr BP (calibrated from Punning et al. 1967, 1981), and similar layers at Petruse with ages around 14 850 ± 350 and 13 940 ± 150 cal yr BP (calibrated from Punning et al. 1981) imply ice advance as late as 13 000 cal yr BP if we consider those organic layers, especially at Viitka, as interstadials, which afterwards were covered with stadial (Haanja) till. The present results and age estimations from Solova, where open sedimentary conditions have persisted since 14 000 cal yr BP, support the conclusion that the unexpectedly young ages from the Viitka intertill organic layer can be regarded as caused by probable slope processes or glaciokarstic slumping where the younger organic material was buried under till as suggested earlier (Karukäpp et al. 1992; Raukas et al. 2004). The ages of Petruse layers, on the other hand, are not contradicting with the ages from Solova, referring to possible ice re-advance around 14 000 cal yr BP (GI-1d), formerly associated with the Older Dryas cooling. Although other evidence around the Haanja Heights, namely accumulation of varved clays in the Tamula basin from 14 700 BP (Kalm 2006) would place Petruse organic layers into the same category of probable slope-processes/glaciokarstic slumping origin as the Viitka layer. The elevated location of Solova (about 170 m a.s.l.) on the Haanja Heights and possibly close to the ice margin of the Haanja stage allows us to use its basal ages as references for deglaciation of the area. On the other hand, Kalm (2006) associated the Haanja stage with minimum ages around 14 700 cal yr BP, taking the corrected age of Tamula clay varve chronology into account (Sandgren et al. 1997). A probable ice-shed line (Karukäpp 2004), better visible along the Haanja and Otepää Heights (less in Pandivere and Vooremaa) and appearing again at Salpausselkä (Lundqvist 1987; Boulton et al. 2009), delimits a narrow NW–SE-trending zone of a possibly thinner and partly inactive glacier that may have been more vulnerable to the Bølling–Allerød warming, as nearly simultaneous breakdown of ice (not necessarily meaning that the area became totally ice-free but rather suggesting that openings in the ice cap developed) occurred in southern Estonia (at Solova prior to 14 000 cal yr BP) and in the north near Haljala and Udriku ca 13 800 cal yr BP (Saarse et al. 2009; Amon & Saarse 2010). However, vegetation development differed markedly along that gradient.

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Hilisjääaegne taimestiku ajalugu ja keskkonnamuutus Solova soo näitel

Leeli Amon, Atko Heinsalu ja Siim Veski

Solova soo hilisjääaegsete setete uurimine näitas, et järveline vabaveeline settebassein moodustus umbes 14 000 kalendriaastat tagasi. On täheldatav lühiajaline soojenemine umbes 13 800 aastat tagasi, taimestik Solova ümbruses oli tundrailmeline vaevakase-drüüase kooslus. Esimene Eesti pinnal leitud pärastjääaegne (puu)kase makrojäänus on umbes 13 500 aastat vana.

PAPER II

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Postglacial palaeoenvironmental changes in the area surrounding Lake Udriku in North Estonia

Leeli AMON and Leili SAARSE

Amon L. and Saarse L. (2010) – Postglacial palaeoenvironmental changes in the area surrounding Lake Udriku in North Estonia. Geol. Quart., **54** (1): 85–94. Warszawa.

Multiproxy data (plant macrofossils, AMS ^{14}C radiocarbon dates, grain-size distribution, loss-on-ignition and magnetic susceptibility) from Lake Udriku Suurjärv in North Estonia were used to interpret local environmental changes during the postglacial period between 13 800 and 11 000 cal yr BP. Sediment lithology is complex but can roughly be described as silt overlain by silty gyttja, gyttja and peat. The macrofossil diagram shows the local vegetation development from Late Glacial pioneer communities to early Holocene communities. The vegetation succession started predominately with *Salix polaris*, which was later replaced by *Dryas octopetala*. The diversity of plant macrofossils increased significantly during the warmer part of the Allerød. Both the diversity and the number of plant macrofossils are low in the Younger Dryas, confirming the severe climatic conditions found during this interval. During the Late Glacial to Holocene transition, aquatic taxa prevail among plant macrofossils. The absence of tree remains among macrofossils of this period suggests that trees were not locally present or were not growing near the studied lake. Proxy data indicate several environmental changes. The sediment composition and vegetation reflect cooler and warmer episodes and confirm that the study area has been free of ice since 13 800 cal yr BP.

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Key words: Lake Udriku Suurjärv, Late Weichselian, macrofossils, lithostratigraphy, AMS ^{14}C dates.

INTRODUCTION

Palaeoecological studies that combine lithological, palaeobotanical and radiocarbon data have successfully determined ice recession chronology and Late Glacial stratigraphy. The Late Glacial stratigraphical subdivision of Estonia comprises two stadials (Older Dryas and Younger Dryas) and one interstadial (Allerød), which are distinguished mainly on the basis of palynological data (Pirrus, 1976; Pirrus and Raukas, 1996). Their chronostratigraphical position has been established by a few radiocarbon dates, thermoluminescence (TL), optically stimulated luminescence (OSL) and ^{10}Be dating of tills and other glacigenic deposits and erratic boulders (Raukas and Stankowski, 2005; Kalm, 2006; Rinterknecht *et al*., 2006; Sohar and Kalm, 2008). Biostratigraphical records in North Estonia have largely dealt with Holocene vegetation dynamics (e.g., Veber, 1961, 1965; Saarse, 1994; Saarse and Liiva, 1995; Saarse *et al*., 1998; Kangur, 2005), while Late Glacial bio- and chronostratigraphy has received limited attention. Up to now only at the Haljala site, 24 km north-east of Udriku, have pollen and chronostratigraphy been studied in detail (Saarse *et al*., 2009). There are two main reasons why radiocarbon dates directly associated with biostratigraphical studies of the Late Glacial are not common. Our Late Glacial deposits are minerogeneous and contain only scarce terrestrial macrofossils suitable for radiocarbon dating. This mostly concerns Northern and Western Estonia where varved clays are widely distributed. At the same time, macrofossil analyses have remained unexploited due to a shortage of analysts and therefore only a few records are currently available from North Estonia for the Late Glacial period (Sohar and Kalm, 2008; Saarse *et al*., 2009). Some random dates from Late Glacial deposits are available, but most are too old as the dating was performed on aquatic mosses (Pirrus, 1976; Saarse and Liiva, 1995; Pirrus and Raukas, 1996).

The present investigation is part of an ongoing project entitled "Environmental and climate changes and their modelling possibilities on the basis of postglacial deposits".The main objective of the present paper is to adjust Late Glacial chronology and examine the local vegetation succession to better understand the regional environmental and climatic variability in

North Estonia. Data on plant macrofossils, loss-on-ignition (LOI) and lithology and AMS ^{14}C dates was used to establish Late Glacial palaeoenvironmental changes.

STUDY AREA

Lake Udriku Suurjärv was examined to adjust the age of the Pandivere ice marginal zone and the chronology of the Late Glacial deposits (Fig. 1). This lake was selected for the study because of the presence of Late Glacial clayey deposits containing plant macrofossils (Saarse, 1994) suitable for AMS ^{14}C dating. The study area is located within the Pandivere ice marginal zone (Fig. 1A) and has an estimated age of 13 300 cal yr BP (Kalm, 2006). Three Udriku lakes (Suurjärv, Väikejärv, and Mudajärv) lie in a V-shaped depression between the Ohepalu–Viitna and Pikassaare–Ohepalu esker ridges (Fig. 1B). These lakes were dammed by esker ridges and their water level was 4 m higher than in Lake Kaanjärv, which is behind the ridge (Fig. 1B).

Udriku Suurjärv is a small (23.7 ha), shallow (6.8 m) lake in NNW Estonia (59°22’17” N, 25°55’50” E) at an altitude of 95.1 m a.s.l. and on the NNW slope of the Pandivere Upland (Fig. 1). The hummocky and rolling landscape on the lake catchment ranges to 115.2 m a.s.l. and mainly composed of sand and gravel, while the surrounding lowland is covered by peat depos-

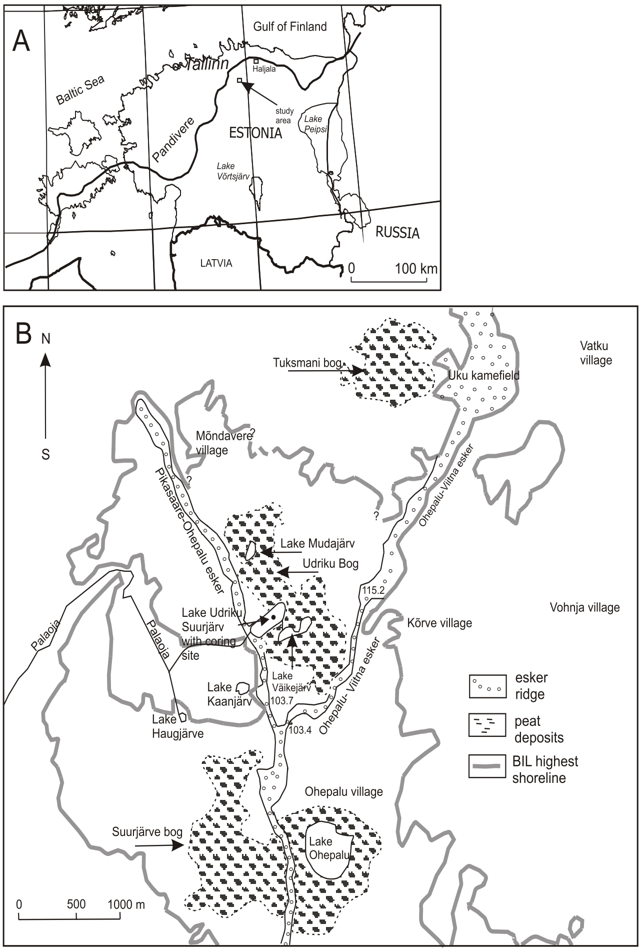


Fig. 1. Location of the study area (A), and coring site (B)

The study site is located within the Pandivere ice marginal zone, indicated by a black line on Figure 1A. The Udriku lakes are located between esker ridges and are surrounded by the Udriku bog. The simulated coastline of the Baltic Ice Lake stage A1 is shown by a thick grey line (B). The question marks point to assumed spillways between Udriku Basin and the Baltic Ice Lake (BIL) its (Fig. 1B). Peaty shores of the lake are strongly abraded and pine trunks and peat cover the narrow NW littoral zone. In the SW part of the region, the Pikassaare–Ohepalu esker borders the coast and forms the sandy shore. This elongated, dystrophic lake is poorly drained. It receives inflow from Lake Udriku Väikejärv and weak temporal outflow occurs via a ditch and the Palaoja Stream (Fig. 1B) to a river in the west. The lake water is reddish-brown, mildly acidic (pH 6.0), rich in organic (33–38 mg $l^{-1}O_2$) compounds and poor in mineral (<10 mg l^{-1}) compounds and water plants (3 taxa; Mäemets, 1968).

The study site belongs to the Boreo-Nemoral Zone, where *Betula pendula*, *Pinus sylvestris* and *Picea abies* are predominant. The esker ridges are covered by a mixed forest of *Picea abies*, *Betula pendula*, *Acer platanoides*, *Populus tremula*, *Fraxinus excelsior*, *etc*. and *Pinus sylvestris* which grows in the bog. The climate in this region is semi-continental. According to the nearest meteorological station, the area has a mean July temperature of 16.5°C, a mean January temperature of –6.7°C and mean annual precipitation of 670 mm yr^{-1} (Jaagus, 2002).

MATERIAL AND METHODS

Studies carried out during the winter of 1989 provided a good understanding of the lacustrine sediment distribution. Coring in the winter of 2009 was performed along a profile described earlier (Saarse, 1994). The sampling site was chosen to be in the middle of the lake at a water depth of 4.4 m (59° 22'17" N, 25°55'50" E), where Late Glacial clayey deposits appeared to be thickest. Five overlapping core segments were extracted using a 1 m long and 10 cm diameter Russian peat sampler. The cores were described and photographed in the field, wrapped in plastic, transported to the laboratory and stored in a cool room. The master core was subject to all analyses. As silt was very poor in macroremains, material from parallel cores, visually correlated with the master core, was used for analyses of plant macrofossils. One-centimetre thick samples for loss-on-ignition (LOI) analyses were taken continuously, while 1 cm thick samples to determine grain-size distribution were taken at 10 cm intervals. Bulk samples for LOI were weighed, dried overnight at 105°C and combusted at 525 and 900°C to calculate moisture, organic matter (OM), carbonate and mineral compounds. The resulting LOI diagram was designed using the *TILIA* and *TGView* programs (Grimm, 1991, 2000). The grain-size distribution for 19 samples was analysed using the *Partica* laser scattering particle size distribution analyser *LA-950V2*. The magnetic susceptibility was measured with a *Bartington MS2E* meter. The sediment surface was cleaned with a microscope glass slide, covered by a thin plastic film and the magnetic susceptibility was measured from the sediment surface at 1 cm resolution.

Macrofossils were extracted by soaking 5 cm thick samples (with a volume range of 160–300 cm^3 and a mean volume of 210–220 cm^3) in a water and $Na_4P_2O_7$ solution and then by sieving the material through a 0.25 mm mesh. The sediment volume was measured in water using a graduated cylinder. Thirty one samples were prepared for analysis and were treated according to the method proposed by Birks (2001). Plant remains were identified under a binocular microscope and their abundance was expressed as concentration by volume. The macrofossil diagram with all of the identified taxa was plotted using the *TILIA* and *TGView* programs.

Three AMS radiocarbon dates from terrestrial plant remains and one date from bulk gyttja were obtained via the Poznań radiocarbon laboratory and provide a chronology for the core studied. Taxa occurring in pioneer vegetation were selected for AMS ^{14}C dating to exclude contamination by younger material and to reduce the danger of using reworked material (Ammann and Lotter, 1988). As recent Late Glacial chronostratigraphy is presented in calendar years (Lowe *et al*., 2008), AMS dates are calibrated and then provided in calendar years using the calibration data set from Reimer *et al*. (2004) and the *CALIB 5.0.1* software (Stuiver *et al*., 2005).

RESULTS AND INTERPRETATION

CHRONO- AND LITHOSTRATIGRAPHY

Altogether four levels in the Udriku sediment sequence were dated by the AMS ^{14}C technique. Three datings of terrestrial macrofossils have age consistent with sediment depth. The date determined from bulk gyttja at the top of the sequence (10 190 ±50) was older than the AMS ^{14}C date below (10 ±60) and not in agreement with the Preboreal–Boreal limit fixed by pollen analyses (Veber, 1965; Saarse, 1994). This led to its rejection from the age-depth model (Fig. 2B). Considering the rapid change in the sediment structure and the number of counted laminae, we suggest that the basal portion of the sediment (800–828 cm) was deposited rather quickly, during a roughly 50 year period.

On the basis of LOI and grain-size distribution results, five lithological units have been identified in the Udriku sequence (Fig. 2A). The sediment colour changed from black at the top through brownish black, olive-grey and green-grey, to grey and dark grey at the bottom of the sequence. The brownish, greenish and olive-grey colours indicate oxic conditions, whereas the greyish colour indicates anoxic conditions (Hahne and Melles, 1997).

Unit Ud-1, **828–800 cm**. The base of the sequence studied consists of laminated clayey silt and is shown by the alternation of beige-coloured fine sand with dark grey clayey silt. The lowest portion of sediment (828–820 cm) has a high clay fraction, with values ranging up to 27% (Fig. 3). Upwards in the sequence, the clay fraction decreases to zero. The AMS ^{14}C date (Table 1) shows deposition at the beginning of the Allerød Interstadial (Fig. 2A).

Unit Ud-2, **800–780 cm**. This unit is dark grey sandy silt containing few plant remains, up to 32% sand, 68% silt, and 4–10% OM. The moisture and OM content show peaks at 782 and 790 cm.

Unit Ud-3, **780–755 cm**, is dark grey weakly laminated silt with a lower OM value (3–6%; Fig. 2A) than in the previous unit. The sand fraction decreased to 13–16%, while the silt fraction increased to 83–87% (Fig. 3).

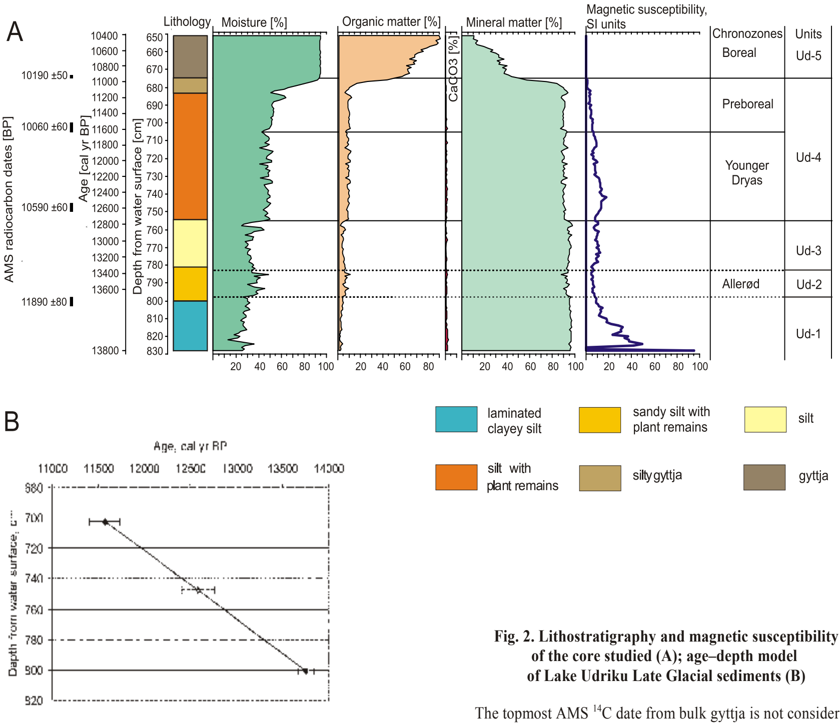


Fig. 2. Lithostratigraphy and magnetic susceptibility of the core studied (A); age–depth model of Lake Udriku Late Glacial sediments (B)

The topmost AMS ^{14}C date from bulk gyttja is not considered, as it does not agree with the following dates

Unit Ud-4, **755–675 cm**, is silt rich in plant remains with 5–10% OM, 17–28% sand and 71–83% silt. Two AMS radiocarbon dates, 12 770–12 410 cal yr BP and 11 750–11 405 cal yr BP (Table 1; Fig. 2B) provide evidence of deposition during the Younger Dryas Stadial. Five beige sandy layers at the basal part of unit Ud-4 coincide with the Allerød/Younger Dryas boundary.

Unit Ud-5, **675–650 cm**, is dark brown gyttja that grades to silt at its lower limit. Sediments in Ud-5 contain 14–20% sand, 80–86% silt (Fig. 3), and up to 90% OM (Fig. 2A).

All samples from the Late Glacial time period were overwhelmingly dominated by high silt fractions, with values ranging from 61 to 86% of the total grain-size distribution (Fig. 3B). The carbonate content was very low, with values of 1–2%, throughout the sediment core studied and the moisture content was in accord with the OM content (Fig. 2A). The average sedimentation rate was about 0.69 mm yr^{-1}during the Allerød Interstadial but decreased to 0.45 mm yr^{-1} during the Younger Dryas.

The magnetic susceptibility values were highest in the basal laminated clayey silt layer (Ud-1), decreased in the uppermost silty deposits and were zero in the gyttja where the mineral particle content decreased from 40 to 20% (Fig. 2A). The most distinct change in magnetic susceptibility was recorded at the transition from laminated clayey silt (glaciolacustrine sediment) to sandy silt (limnic sediment).

MACROFOSSILS

In the current study, attention was paid to macrofossil assemblages in the Late Glacial sediments (Fig. 4), which are a good indicator of local vegetation and water level changes (Digerfeldt, 1988; Gaillard and Birks, 2007). Besides taxa, the content of coarse detritus is a valuable component in macrofossil analyses. This is because sediment deposited in shallow water and close to the shore contains a larger amount of coarse detritus from terrestrial plant remains than deep-water sediments do (Digerfeldt, 1988). The section analysed covers the approximate time span of 13 800–11 000 cal yr BP (Fig. 4). The temporal resolution of plant macrofossil samples was high, especially in the lowermost portion where approximately two hundred years are represented by seven samples (Fig. 4). The plant macrofossil assemblage from Lake Udriku consists of 25 plant species and genera, with the dominant species typically represented by cold-tolerant and boreal plants. Two Charales were also identified. The macrofossil diagram was divided into five zones and displayed several sharp changes (Fig. 4).

In the lowermost zone MA-1 (828–800 cm) five plant taxa were recognized: individual *Silene* sp., *Ranunculus* sect *Batrachium* and *Nitella*, a small number of *Dryas octopetala* and abundant *Salix polaris* leaf fragments (Fig. 4). One sample also contained cladoceran (*Daphnia*) remains. The number of *Salix polaris* decreased sharply and the *Dryas octopetala* curve

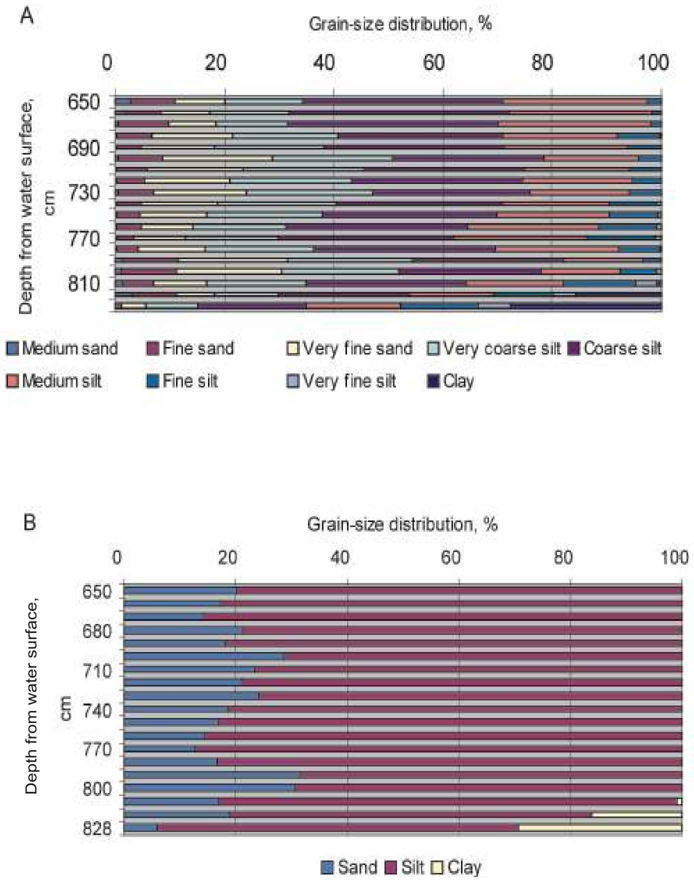


Fig. 3. Grain-size distribution of Lake Udriku sediments (A) with indication of the summary grain-size (B)

increased at the zone upper limit. At the core depth of 822–821 cm increased coarse detritus has been observed.

In zone MA-2 (800–780 cm) seven different plant taxa were recorded, with *Dryas octopetala* leaves and *Daphnia* spp. ephippia being present throughout.

The next zone MA-3 (780–755 cm) was rich in macroremains and a total of 18 taxa were identified. *Dryas octopetala*, *Ranunculus* sect *Batrachium* and *Nitella* were represented continuously and had maxima in this zone, but other taxa (Poaceae, Asteraceae, *Saxifraga etc*.) occurred sporadically and in low amounts. *Daphnia* spp. ephippia was still continuously present.

Zone MA-4 (755–705 cm) was characterized by a low abundance and number of plant remains. Only *Nitella* was present throughout the lower portion of the zone, but it decreased abruptly at a core depth of 740 cm. In the upper portion of the zone (735–705 cm), the light-demanding *Dryas octopetala* reappeared and has a slight peak, whereas *Ranunculus* sect *Batrachium* and *Nitella* oospores disappeared. The total number of identified fossils decreased to six. *Daphnia* occurred only sporadically in this zone.

In the topmost zone MA-5 (705–675 cm) different species of *Potamogeton* appeared and the *Ranunculus* sect *Batrachium* concentration increased slightly. *Potamogeton filiformis* is regarded as an alkaliphilous species, which occurs today in the large Estonian lakes Peipsi and Võrtsjärv as a relic from the Late Glacial period (Mäemets, 2002). The topmost portion of sediment 675–650 cm (unit Ud-5) was not examined.

DISCUSSION

DEGLACIATION PATTERN

The calibrated radiocarbon ages from terrestrial macroremains were in correct stratigraphic order and con-

Table 1

AMS ^{14}C dates from the Lake Udriku sequence

Sample depth [cm]	^{14}C age [yr BP]	Lab. number	Cal. ^{14}C age [yr BP] 68% probability	Dated material
675–673	10 190 +50	Poz-31429	11 990–11 805	Bulk gyttja
705–700	10 060 +60	Poz-30769	11 750–11 405	*Dryas* leaves
750–745	10 590 +60	Poz-30429	12 770–12 410	*Dryas* leaves
803–798	11 890 +80	Poz-30430	13 835–13 665	*Dryas* leaves

strained the start of the lacustrine sedimentation. The age-depth model presented in Figure 2B is in good agreement with the model from the Haljala site (Saarse *et al*., 2009), supporting the idea that ice retreated from the northern slope of the Pandivere Upland not later than 13 800 cal yr BP. This is 300–500 years earlier than previously suggested (Vassiljev *et al*., 2005; Saarse *et al.*, 2007; Rosentau *et al*., 2009). The ice recession could have occurred even earlier, as lacustrine sedimentation may be delayed by a hundred years (Warner *et al*., 1991). The AMS ^{14}C dates from Udriku and Haljala were consistent with the ice position chart, which indicates that the Udriku area deglaciated at almost the same time as Haljala (Ramsay, 1929; Rähni, 1961).

The esker ridges, kame fields and the Udriku depression between them were formed during the ice retreat from the northern slope of the Pandivere Upland (Fig. 1). Obviously, eskers melted out of the ice first and were followed by kame fields and glaciodepressions. The AMS ^{14}C date from the basal clayey silt (803–798 cm, 13 750 ±85 cal yr BP, Poz-30430) matches the Allerød age and corresponds to the OSL date for sand from the Pikassaare kame field (13 700 yr BP; Raukas and Stankowski, 2005). However, the AMS ^{14}C date is about 700 years older than the ^{10}Be date (13 060 ±1120, EST-12; Rinterknecht *et al*., 2006) of the Kallukse Lodikivi boulder from 7.5 km east of Lake Udriku. Thus, we suggest that the Lake Udriku Basin was established not later than 13 800 cal yr BP as a sheltered bay of the Baltic Ice Lake (BIL), which (according to reconstruction) invaded areas below 90 m a.s.l. (Vassiljev, pers. comm.). The palaeogeographic reconstruction did not firmly establish the connection between the BIL and the Udriku Basin, as the threshold of the latter is covered by peat of unknown thickness. Therefore, peat was not removed from the simulated water surface and the possible spillways in Figure 1B are denoted by a question mark. However, laminated sediments in the bottom of the Udriku Basin, which were deposited when the remnants of the ice melted, indicate a connection between Udriku Basin and the BIL.

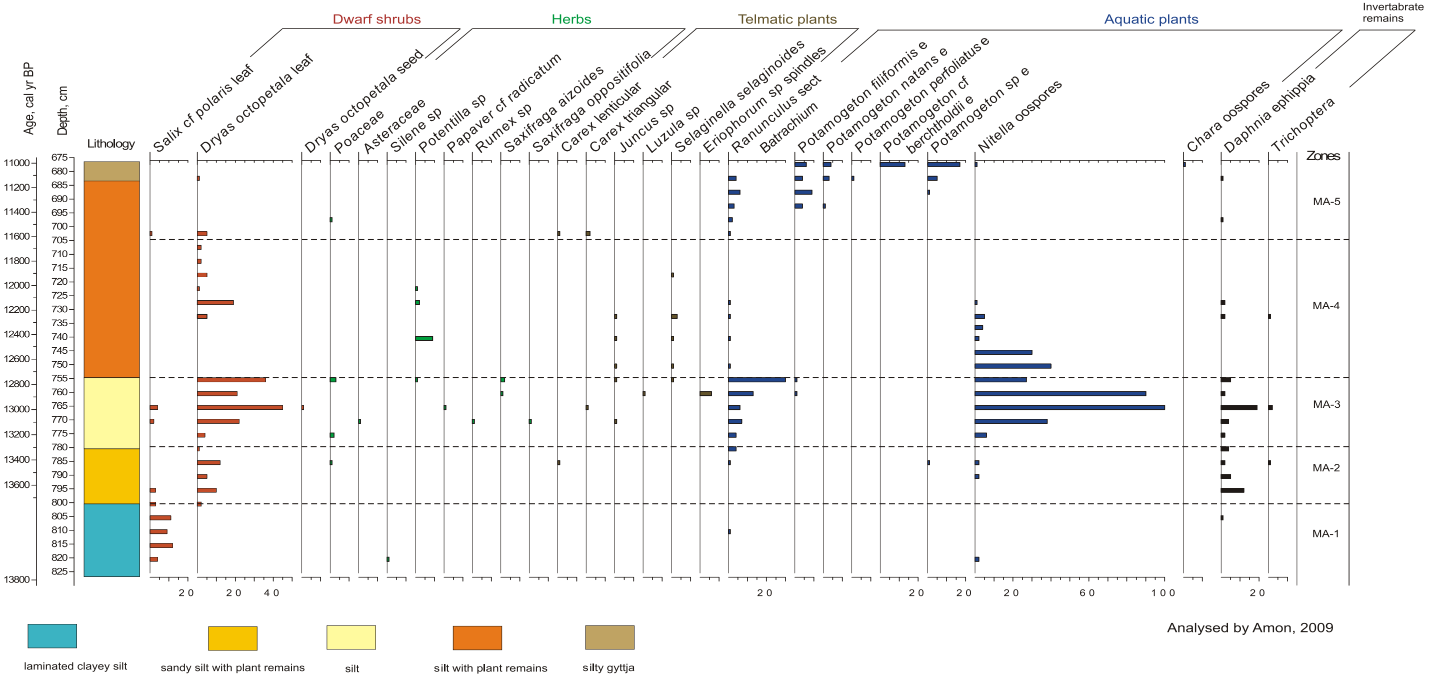
PALAEOENVIRONMENTAL CHANGES

ALLERØD

The Lake Udriku sediment record began 13 800 cal yr BP with clayey silt deposition containing low amounts of OM (Fig. 2A). The minerogenic material content, carried into the basin from the melting ice remnants and surrounding esker ridges, was high. The macrofossil diagram is relatively poor in taxa (MA-1, Fig. 4), indicating periglacial conditions with nearly bare ground close to a widespread occurrence of dead ice and permafrost. The dominant species was *Salix polaris*, which has been reported as a pioneering dwarf shrub in studies of northern areas (Birks, 1994) and Southern Sweden and Denmark (Bennike *et al*., 2004). However, these typical snow-bed dwarf shrub leaves may be over-represented in sediments due to their large number and good preservability (Korsager *et al*., 2003). As sedimentation took place in a lagoon of the BIL, the past lake level, the high sedimentation rate and barren soils may have also influenced the macrofossil composition (Väliranta, 2006*a*, *b*).

A sharp increase in the sandy fraction at a core depth 800 cm (*ca*. 13 700 cal yr BP) obviously corresponds to the isolation contact that resulted in the separation of Lake Udriku from the BIL and the formation of different water bodies. At this contact, the sand fraction content increased from 18 to 31% (Fig. 3B) and the magnetic susceptibility decreased considerably (Fig. 2A), indicating a change in the sediment source during the isolation event. At the same time, a notable change in the vegetation assemblages occurred: *Salix polaris* remains disappeared almost completely and were replaced by *Dryas octopetala*, which is another plant species common in Late Glacial sediments (MA-2, Fig. 4). The remainder of the plant assemblages consisted of a few grasses and sedges. According to Lowe *et al*. (2008), this corresponds to GI-1b, a short cooling episode within the so-called Allerød warming.

The next zone (MA-3, Fig. 4) is characterized by a variable vegetation succession. The dominant terrestrial species was still *Dryas octopetala*, occurring among relatively abundant macroremains. The assemblage consisting of *Papaver, Rumex* and two species of *Saxifraga* reflects suitable conditions for the development of variable terrestrial plant cover. Conversely, the presence of telmatic species such as *Carex, Juncus* and *Luzula* indicates the proximity of wetland. In this zone, aqueous organisms were also represented in larger numbers. *Ranunculus* sect *Batrachium* seeds were abundant, as were oospores of the stonewort genus *Nitella*. Both of these aquatic species are common colonisers of newly formed water bodies and are usually found in large quantities (Birks, 2000). In the Udriku sequence, *Nitella* was first recorded at about 13 800 cal yr BP and *Ranunculus* sect *Batrachium ca*. 13 750 cal yr BP, but their maxima occurred later: *Nitella* had a peak *ca*. 13 000 cal yr BP, and *Ranunculus* sect *Batrachium* peaked at the end of the Allerød (Fig. 4). As for water plants, *Potamogeton filiformis*



Analysed by Amon, 2009

Fig. 4. Plant macrofossil diagram from Lake Udriku, displaying macrofossils (number of specimens per sample)

m – megaspore (*Selaginella selaginoides*), e – endocarp (Potamogetonaceae); sedges (*Carex*) are divided into two types based on their morphology: triangular-shaped and lens-shaped seeds were found, which have a short lag time because they are generated every year, are dispersed by water and are therefore not dependent on soils (Iversen, 1954). The mean July temperature could have been about 8–10°C considering the temperature requirements that allow *Potamogeton filiformis* and *Ranunculus* sect *Batrachium* to generate during this warmer episode (Isarin and Bohncke, 1999; Gaillard and Birks, 2007). In conclusion, the increased temperature during the Allerød warming obviously affected water plant distribution in Lake Udriku and accumulation of organic debris in the sediments. The light-demanding *Dryas octopetala* was present in significant amounts and the landscape around Lake Udriku was likely open during this period.

YOUNGER DRYAS

The temperature decreased during the Younger Dryas stadial (12 700–11 600 cal yr BP), especially in wintertime (Denton *et al*., 2005), due to a shift of the North Atlantic polar front (Bard *et al*., 1987; Alley, 2000), which brought about the dominance of herb and shrub vegetation, at least in the areas surrounding Haljala (Saarse *et al*., 2009). At the Allerød–Younger Dryas lithostratigraphic boundary (755 cm), moisture and OM content slightly increased and mineral compounds decreased (Fig. 2A). Increasing sand fraction proportions (Fig. 3) suggest a lowering of the water level and the erosion of the exposed sandy shores to a greater extent than was previously seen. The abundance and diversity of macroremains declined (MA-4, Fig. 4), as relatively cool climate inhibited the spread of aquatic plants and animals (Birks, 2000).

The reaction of vegetation during the Younger Dryas stadial (Ma-4) can be separated into two parts. *Dryas octopetala* and *Ranunculus* sect *Batrachium*, two dominant plant species of the previous warming episode, disappeared in the lower part of MA-4 (Fig. 4). The macrofossils that were found consisted of a few species of different herbs and telmatic plants (*Potentilla* sp*., Juncus, Selaginella selaginoides*) and a decreased number of *Nitella* oospores. In the upper part of Ma-4, at 12 300 cal yr BP, *Dryas octopetala* reappeared confirming tundra-like conditions. The drop in the abundance of *Nitella* oospores in samples may indicate unfavourable water conditions and prolonged ice cover (Birks, 2000; Kultti *et al*., 2003). The establishment of treeless shrub tundra with herbs, especially open habitat taxa, shows a reversal to colder and drier conditions (Pirrus and Sarv, 1968; Saarse *et al*., 2009) and is described as "steppe tundra" on the Karelian Isthmus (Subetto *et al*., 2002).

EARLY HOLOCENE

The beginning of the Holocene is shown in the Udriku section at 11 600 cal yr BP (705 cm) by a silt layer deposition (Fig. 2A). The transition from the Younger Dryas to the Holocene is distinct in changes in plant community (MA-5, Fig. 4). The characteristic arctic species, *Dryas octopetala*, almost completely disappeared, while *Ranunculus* sect *Batrachium* reappeared together with different species of the genus *Potamogeton*. The mean summer temperature could have been above 9°C, referring to the *Potamogeton perfoliatus* modern range limit at the Arctic tree-line (Bennike *et al*., 2004). *Daphnia* ephippia and the first single oospore of the genus *Chara* were found in this zone.

The sedimentation change in Lake Udriku at the Preboreal–Boreal limit, about 11 000 cal yr BP, coincides with the start of peat accumulation in the bog surrounding the lake (Veber, 1965). The topmost black gyttja in Lake Udriku (Fig. 2A) was mostly formed from decomposed organic debris and humic acids that infiltrated into the lake from the surrounding bog. The elemental composition of gyttja showed organic carbon saturation (C_{org} – 44–58%), but a low content of nitrogen compounds (1.4–2.0%; Saarse, 1994). This elemental composition and C/N ratio is typical of peat and peaty gyttja that is still depositing in the littoral zone of a lake.

TREE-LINE ADVANCES IN NORTHERN ESTONIA

Tree-line dynamics during the Late Quaternary have been discussed in several studies using plant macrofossil data or macroscopic charcoal (Willis and van Andel, 2004; Binney *et al*., 2009). Unfortunately, not much macrofossil data is available from the south-east sector of the last glaciation. Recent data from Latvia (Heikkilä *et al*., 2009) and Southern Estonia adds information about the reintroduction of tree species following the glaciation in the eastern Baltic. Plant macrofossil analysis from two localities of Southern Estonia confirmed the reintroduction of *Betula* sect *Albae* (tree birch) at 13 500–13 400 cal yr BP. The Lake Udriku record (about 200 km north of these localities), however, did not show tree birch immigration during the Late Glacial period and thus suggested local treeless vegetation. As the coring site is located in the central part of the lake, the macrofossil record cannot adequately reflect vegetation on the terrain. In contrast to Udriku, the Haljala pollen record indicated that a woody tundra environment was already present in the Allerød (Saarse *et al*., 2009). The ground layer contained *Artemisia*, Chenopodiaceae, Poaceae, Carophyllaceae and Asteraceae, whereas *Betula* and *Pinus* could have formed sparse woody stands where heliophytic species had developed (Saarse *et al*., 2009). Still, according to Birks and Birks (2000), pollen data should be handled with caution in Late Glacial studies.

In many studies focussing on the Late Glacial period the vegetation record begins with aquatic plants (Birks, 2000; Wohlfarth *et al*., 2002; Subetto *et al*., 2002). This is not the case in Udriku, where *Salix polaris* was the prevalent macrofossil in the lower part of the sequence. Aquatic plants were present in larger quantities later in the Allerød, but disappeared almost completely in the Younger Dryas. Patterns similar to the Udriku macrofossil record and plant succession were described for Russian Karelia (Lake Tambichozero), where lacustrine sedimentation also started 13 700 cal yr BP (Wohlfarth *et al*., 2002). The lower part of the core contained a plant community similar to that of Lake Udriku (dwarf shrubs, grasses, *Nitella* oospores). Another similarity is the absence of trees during the warmest period of the Allerød. The first occurrence of the seeds of *Betula pubescens* (tree birch) in Lake Tambichozero was recorded at approximately 11 000 cal yr BP (Wohlfarth *et al*., 2002), but in the

Llet-Ti site (Usa Basin, northern taiga) it was already seen at approximately 12 700 cal yr BP (Väliranta *et al*., 2006).

CONCLUSIONS

1. Plant macrofossils, AMS ^{14}C dates and lithological parameters were used to interpret the environmental history of Lake Udriku from the Late Glacial period to the Holocene.

2. Five lithostratigraphical units were differentiated. These units vary in grain-size distribution, LOI results and magnetic susceptibility.

3. The macrofossil diagram shows the local vegetation development from Late Glacial pioneer communities to early Holocene communities.

4. By 13 800 cal yr BP, the surroundings of Lake Udriku were freed of ice. This is confirmed by the age and finds of *Salix polaris* and *Dryas octopetala* remnants in limnoglacial sediments.

5. The diversity of identified plant taxa was highest in the Allerød warm episode between 13 100 and 12 700 cal yr BP and decreased considerably during the Younger Dryas.

6. A distinct change in plant community at about 11 600 cal yr BP indicates the major climatic warming.

7. Both the Haljala and Udriku sites show evidence that the northern slope of the Pandivere Upland deglaciated by 13 800 cal yr BP. This is approximately 500 years earlier than has been previously suggested.

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PAPER III

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Timing of Lateglacial vegetation dynamics and respective palaeoenvironmental conditions in southern Estonia: evidence from the sediment record of Lake Nakri

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ABSTRACT: This paper investigates a detailed well-dated Lateglacial floristic colonisation in the eastern Baltic area, ca. 14 000–9000 cal. a BP, using palynological, macrofossil, loss-on-ignition, and ^{14}C data. During 14 000–13 400 cal. a BP, primarily treeless pioneer tundra vegetation existed. Tree birch (*Betula* sect. *Albae*) macro-remains and a high tree pollen accumulation rate indicate the presence of forest-tundra with birch and possibly pine (*Pinus sylvestris* L.) trees during 13 400–12 850 cal. a BP. Palaeobotanical data indicate that the colonisation and development of forested areas were very rapid, arising within a period of less than 50 years. Thus far, there are no indications of conifer macrofossils in Estonia to support the presence of coniferous forests in the Lateglacial period. Signs of Greenland Interstadial 1b cooling during 13 100 cal. a BP are distinguishable. Biostratigraphic evidence indicates that the vegetation was again mostly treeless tundra during the final colder episode of the Lateglacial period associated with Greenland Stadial 1, approximately 12 850–11 650 cal. a BP. This was followed by onset of the Holocene vegetation, with the expansion of boreal forests, in response to rapid climatic warming. Copyright © 2011 John Wiley & Sons, Ltd.

KEYWORDS: Lateglacial pioneer vegetation; pollen; plant macrofossils; corrosion index; deglaciation; Estonia.

Introduction

During the last termination, abrupt and distinct climatic oscillations occurred (Walker *et al.*, 1999). The transgressiveness of such palaeoclimatic events in time and space requires synchronisation within the North Atlantic region with respect to the last termination. In recent years, this process of synchronisation has made tremendous strides (Rasmussen *et al.*, 2006; Lowe *et al.*, 2008). The retreat of the Scandinavian Ice Sheet (SIS) and the changing climate has triggered major shifts in terrestrial vegetation ecosystems. Lateglacial vegetation succession was influenced by a combination of factors, including the Weichselian deglaciation pattern (Kalm, 2006; Rinterknecht *et al.*, 2006), the regional migration rate of plants (Huntley and Birks, 1983; McLachlan *et al.*, 2005; Pearson, 2006; Svenning *et al.*, 2008), local plant succession, soil development (Egli *et al.*, 2006), and climatic change.

The history of deglaciation, in particular the timing and pattern, of the eastern Baltic region is still under debate (Zelcs and Markots, 2004; Kalm, 2006; Rinterknecht *et al.*, 2006, 2008). The geographical location of Estonia in the southeastern sector of the SIS has generated further interest in formulating a detailed chronology of the deglaciation history of Estonia. Such information would contribute towards better characterising the movements and retreat of the second largest ice sheet complex of the former Northern Hemisphere ice sheets (Rinterknecht *et al.*, 2006). The history of Estonian Lateglacial vegetation and deglaciation has been studied for over a century, yet the latest synopsis (Raukas, 2009) indicates that the age scale is insufficient and unreliable. Another issue is the lack of adequately dated biostratigraphical reference sites that might serve as the basis for chronologically precise palaeoenvironmental reconstructions. Although there are about 100 absolute age estimations from Estonian Lateglacial sediment sequences (Kalm, 2006), only a few may be associated with biostratigraphical studies. Consequently, almost all of the Lateglacial sequences in Estonia and the eastern Baltic area are, in general, not independently dated, and are solely described by the comparison of pollen zones and pollen percentage data (Thomson, 1935; Pirrus, 1969, 1971). Moreover, ^{14}C-dated investigations of Lateglacial vegetation succession in latitudinally adjacent areas do not exist, with the exception of some sites in eastern Karelia (Wohlfarth *et al.*, 1999, 2004, 2007), Latvia (Heikkilä *et al.*, 2009), and Lithuania (Stancikaite *et al.*, 2008, 2009).

The aims of the present study were to (i) reconstruct the migration of pioneering plant species into areas that were formerly covered by an ice sheet, (ii) describe floral development at a good temporal scale, and (iii) demonstrate vegetation response to oscillations in the climate during the Lateglacial period ca. 15 000–11 700 cal. a BP. To accomplish this objective, we combined high-resolution pollen records with macrofossil evidence and an accelerator mass spectrometry (AMS) ^{14}C-dated sediment sequence from southern Estonia in the Baltic area.

Study site

A new Lateglacial site was used for the purpose of this investigation, specifically Lake Nakri (0.9 ha, 48.5 m a.s.l., 57° 53.703′ N, 26° 16.389′ E), which is situated in southern Estonia (Fig. 1). Lake Nakri is a small shallow hard-water lake that is 3.2 m deep. The lake basin, which has a catchment area of less than 0.25 km^2, lies in front of the Otepää ice marginal zone, which formed during the retreat of the ice sheet margin ca. 14 700–14 500 cal. a BP (Sandgren *et al.*, 1997; Kalm, 2006). The lake is surrounded by slightly rolling glacial topography, with the local Otepää stage end moraine reaching up to 61 m a.s.l. near the lake. Fen and mixed conifer forest surround the lake. The modern mean air temperature in the region is 5.5°C (mean July temperature 17.0°C; mean January temperature −4.9°C).

Palaeogeographical modelling (Rosentau, 2006) suggests that Lake Nakri is at the edge of a larger proglacial lake (the so-called Laatre basin) that rose more than 20 m above the present lake level, and drained in a southwesterly direction away from the retreating glacier into the valley of the River Gauja.

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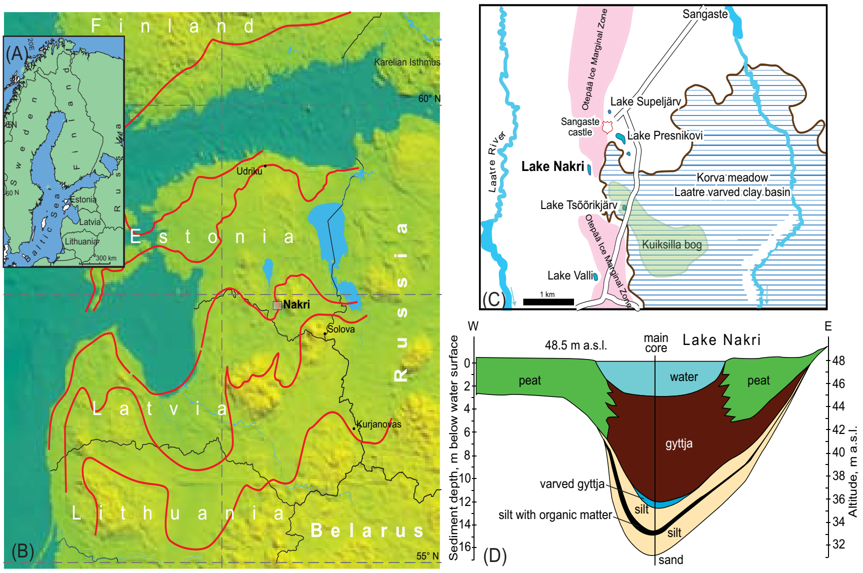

Figure 1. (A) Regional scheme of the Baltic region. (B) Map of the eastern Baltic area showing Lateglacial sites discussed in the text (Amon *et al.*, 2010; Amon and Saarse, 2010; Heikkilä *et al.*, 2009; Subetto *et al.*, 2002), with the location of SIS ice marginal zones (compiled from Raukas *et al.*, 1995; Zelcs and Markots, 2004; Kalm, 2006). (C) The area around Lake Nakri. (D) W–E sediment cross-section from Lake Nakri, showing location of the main analysed sediment core. This figure is available in colour online at wileyonlinelibrary.com.

Material and methods

Coring and lithostratigraphy

Using a Russian corer, parallel overlapping sets of 1 m long segments of the lake sediment sequence, extending 16.56 m from the ice surface, were recovered by coring at the deepest point of the lake (3.2 m) in February 2007. The core was described and photographed in the field, and subsequently transported to the laboratory for further analysis and documentation. The organic matter content of the sediment was determined by loss-on-ignition (LOI) at 550°C for 4 h (Heiri *et al.*, 2001). Measurements were performed on continuous 1 cm thick subsamples.

Palaeoecological methods

Pollen subsamples of known volume (0.5–2 cm^3) and thickness (1 cm) were taken at 5–10 cm intervals from a core depth of 1656–1050 cm. Pollen sample preparation followed a standard acetolysis method (Berglund and Ralska-Jasiewiczowa, 1986) combined with cold concentrated HF treatment to remove inorganic matter (Bennett and Willis, 2001). *Lycopodium* spores were added to calculate pollen concentration and subsequently the pollen accumulation rate (PAR) values (Stockmarr, 1971). At least 500 terrestrial pollen grains were counted at each subsample level, except for the four lowest level samples, where only about 200 grains were observed due to low pollen concentrations. *Betula nana* type was differentiated from *Betula* on the basis of size and morphology (Mäkela, 1996; Caseldine, 2001). Corroded and degraded grains of smooth-surfaced pollen types such as *Betula*, *Alnus*, and *Corylus* were counted separately during routine pollen analysis and used as measures of redeposition or inwash from older sediments (Birks, 1970). Pollen data were expressed as percentages of the total terrestrial pollen sum, and PAR values were expressed as pollen grains cm^{-2} a^{-1}. Counts of spores, green algae, charcoal, and other microfossils were calculated as percentages of the total sum of terrestrial pollen.

Plant macrofossil analysis was performed at contiguous 2.5 cm intervals from more organic-rich sediments at core depths of 1500–1475 cm and 1304–1250 cm, and at contiguous 5 cm intervals from inorganic silty/clay-like sediments at core depths of 1635–1510 cm and 1475–1304 cm. In addition, three subsamples were taken from the overlying gyttja at core depths of 1226, 1201, and 1161 cm. The preparation for plant macrofossil analysis followed conventional procedures (Birks, 2001). The uniform subsample size (100 cm^3) was determined by water displacement in a measuring cylinder. Samples were wet sieved through mesh of 0.25 and 0.12 mm. Clay-like sediment samples were soaked in $Na_4P_2O_7.H_2O$ solution overnight to disintegrate fine-grained inorganic particles and to improve the ease of sediment sieving. Material retained on the sieves was examined using a stereo and light microscope. In addition to plant macrofossils, several limnic animal remains were also identified and counted. Relevant literature, atlases (Beijerinck, 1976; Cappers *et al.*, 2006; Mossberg and Stenberg, 2006), and reference collections (Institute of Biology, University of Bergen, and Department of Environmental Archaeology, Danish Prehistory, National Museum of Denmark) were used for plant macrofossil identification. Remains of birch tree-types (*Betula pendula* and *B. pubescens*) were grouped as *Betula* sect. *Albae*. *Carex* seeds were divided into two groups by seed morphology: triangular seeds and lenticular seeds.

Chronology

Terrestrial plant macrofossils (preferably small branches, *Dryas* leaves, and *Betula* catkin scales), which were identified during

Table 1. Radiocarbon dates of samples from Lake Nakri sediment core. The weighted average ages of the deposition model in OxCal 4.1. (Bronk Ramsey, 2001; Reimer *et al.*, 2004) in column 5 were used in the age–depth model.

Depth below water/ice surface (cm)	Lab code	^{14}C date	Calibrated age (cal. a BP, 2σ)	Age (cal. a BP) deposition model, weighted average	Dated material
1169	Poz-20611	8870 ± 50	9970 ± 200	9970 ± 125	Wood fragment
1241	Poz-20612	9610 ± 60	10 965 ± 210	11 105 ± 65	Terrestrial plant macrofossils
1272	Poz-20076	10 150 ± 50	11 825 ± 220	11 610 ± 125	Wood fragment
1422.5	Poz-22639	10 510 ± 60	12 440 ± 180	12 575 ± 45	Wood fragment
1462	Poz-20077	10 800 ± 40	12 830 ± 45	12 830 ± 20	Wood fragment
1497	Poz-20526	11 430 ± 70	13 290 ± 130	13 325 ± 55	Terrestrial plant macrofossils
1520	Poz-20528	11 660 ± 70	13 520 ± 175	13 470 ± 55	Terrestrial plant macrofossils
1545	Poz-20613	11 810 ± 80	13 665 ± 220	13 575 ± 55	*Dryas* leaves
1630	Poz-20529	12 060 ± 70	13 920 ± 150	13 925 ± 80	Terrestrial plant macrofossils

the course of macrofossil analysis, were radiocarbon dated by using the AMS method in the Poznan Radiocarbon Laboratory (Poz), Poland (Table 1). The chronology of the Lake Nakri sediment sequence was based on the weighted average calibration of AMS radiocarbon dates (0 = AD 1950), which were derived from the INTCAL dataset (Reimer *et al.*, 2004). Nine levels of terrestrial plant remains were fitted to the OxCal 4.1 (Bronk Ramsey, 2001) deposition model (Bronk Ramsey, 2008) at the 2σ confidence level. The deposition model allowed lithostratigraphical boundaries to be incorporated into the age–depth curve (Fig. 2). Stratigraphic age estimates from both ends of the deposition model were extrapolated.

Statistical methods

Pollen diagrams and macrofossil data were compiled using Tilia 1.0.1 (Grimm, 2007). Zonation was based on the binary splitting of the sum-of-squares method using the PSIMPOLL 4.10 program (Bennett, 2002). The significance of statistically determined zones was estimated by comparison with the broken-stick model described by Bennett (1996). Macrofossil zonation using PSIMPOLL is based on macrofossil data for vascular plants.

Down-core ordination by detrended correspondence analysis using Canoco for Windows 4.5 (ter Braak and Smilauer, 1998) yielded a compositional gradient length of the dataset of more than 2 standard deviation units (2.26 SD), showing that the dataset has a primarily linear structure, and suggesting that correspondence analysis (CA) may be the appropriate ordination method to summarise the pollen data. CA ordination in Canoco and CanoDraw 3.10 (Smilauer, 1994) was applied after deleting minor taxa that did not reach a value of 0.5%.

Results

Litho- and chronostratigraphy

The Lateglacial to early Holocene sediments of Lake Nakri that were investigated were divided into six lithostratigraphical units (Fig. 2), of which the lowermost unit 1 (1656–1500 cm) was beige silt that became increasingly sandy towards the bottom (possibly varved clay). Unit 2 (1500–1464 cm) was black-coloured silt with up to 7% organic matter. Unit 3 (1464–1262 cm) was again organic-poor beige clay-like silt/silty clay that became more organic-rich towards the upper limit, changing into the black coarse detritus (peaty) gyttja of unit 4 (1262–1240 cm). Unit 5 (1240–1207 cm) was distinctly laminated gyttja (possibly varved, LOI, >25%) that gradually turned into the homogeneous brown gyttja of unit 6 (1207–320 cm; i.e. top of the sediment).

Evidence from the deposition model, which incorporated the nine AMS dates of terrestrial macrofossils, suggests that sedimentation of the organic-poor sandy silt (LOI ~2.5%) in unit 1 started a little earlier than 14 000 cal. a BP. The minerogenous silts of units 1 and 3 accumulated throughout the recorded Lateglacial period, spanning 14 050–11 650 cal. a BP. This accumulation was interrupted by a layer of organic-rich silt in unit 2, which was deposited between 13 500 and 12 800 cal. a BP. The gyttja sediments accumulation started in the beginning of the Holocene.

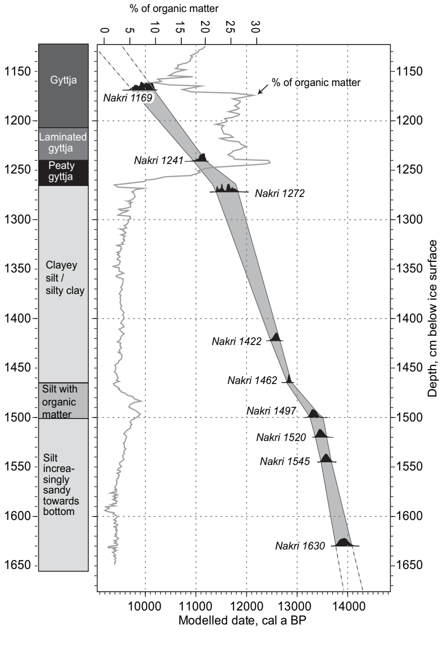

Figure 2. Lithostratigraphic column, organic matter content, and age–depth model for Lake Nakri sediments using lithostratigraphical boundaries. Depth is the variable, and the deposition is assumed to be a Poisson process. Extrapolated age estimations are represented by broken lines.

Pollen and plant macrofossil record

The pollen record of Lake Nakri comprised of 71 sample levels (and 88 microfossil types), which were divided into five statistically significant (local) pollen assemblage zones (PAZ); the lower three zones roughly corresponded to the boundaries of the lithostratigraphical units (Table 2 and Fig. 3).

Corroded and degraded grains of smooth-surfaced pollen types, such as *Betula*, *Alnus*, and *Corylus*, were recorded in the pollen analysis as a measure of redeposition or inwash from older sediments; these grain counts showed a reversed distribution in comparison with LOI values and the relative abundance of tree pollen types. Corroded pollen grains appeared simultaneously with the relative abundance of terrestrial fungal remains, further supporting that their origin was inwashed. Most of the *Alnus* and *Corylus* pollen in the organic-poor matter of Lateglacial deposits appeared corroded. The corrosion of birch pollen ranged from below 10% in unit 2 to 40% in unit 1. Other pollen that was exotic to the Lateglacial environment, including thermophilous tree taxa, such as *Tilia*, *Quercus*, *Fraxinus*, and *Carpinus*, in addition to *Picea*, were also presumably inwashed from older deposits. The inwash of birch and pine pollen in quantities comparable to the corrosion index of *Betula* might be expected to the extent that this proportion of inwashed pollen should be removed from calculations of PARs and interpretations of forest cover during the Lateglacial period. The goodness-of-fit (R^2) between the abundance data for inwashed thermophilous pollen and corroded *Betula* was 0.463 (Fig. 4).

During macrofossil analysis, 33 different species (or families) were identified (Table 3 and Fig. 5). The basal part of the studied section (1650–1635 cm) did not contain macrofossils.

Discussion

Reconstruction of the vegetation and palaeoenvironment at Lake Nakri

To date, the ‘classical’ established Estonian Lateglacial pollen stratigraphy generally documents Older Dryas Arctic conditions, an Allerød warming with up to 80% of pine pollen, a Younger Dryas herb-dominated cooling, and a subsequent Holocene warming (Pirrus, 1969, 1971). Ongoing research of Lateglacial vegetation succession in Estonia has located several Lateglacial sections dating back to 14 000 cal. a BP. Lake Nakri has yielded a complex and trustworthy high-resolution signal for Bølling/Allerød (Greenland Stadial (GS)-1) warming, which includes PAR and parallel macrofossil investigations to separate the local and regional vegetation signal in the barren glacial landscape. The percentage values of Lateglacial pollen types have proven to be insufficient for elucidating the real vegetation composition (Davis and Deevey, 1964). Therefore, in the current study, we primarily used PARs and macrofossil data for vegetation reconstruction. However, even pollen PAR values are not entirely reliable (Giesecke and Fontana, 2008), especially in the Lateglacial period. This is because the values are negatively influenced by sediment focusing (Davis *et al.*, 1984) and resedimentation (Iversen, 1936) caused by low pollen production and high sedimentation rates (Seppä, 1996; Seppä and Hicks, 2006). Hence the use of plant macrofossil analysis is suitable for local vegetation reconstruction, especially for the Lateglacial period (Birks and Birks, 2000), as well as supplying material for AMS dating.

14 050–13 400 cal. a BP: treeless pioneer tundra

It was inferred from the deposition model that the area around Lake Nakri, immediately south of the Otepää ice marginal zone, deglaciated just before 14 000 cal. a BP. This event may be linked with the onset of Greenland Interstadial (GI)-1c (13 954 ± 165 a before AD 2000 AD; Lowe *et al.*, 2008), for which a regional warming episode within the Lateglacial period was recorded. Although the initial development of flora and landscape around the Nakri basin corresponds to the relatively warm phase, the preserved palaeobotanical proxy indicates the presence of colder vegetation types. The combination of corroborating evidence from macrofossil and pollen analysis shows that *Betula nana*, *Salix herbacea*, *Dryas octopetala*, *Saxifraga* sp., *Empetrum nigrum*, *Artemisia*, *Helianthemum nummularium*, and Chenopodiaceae dominated the shrub and herb tundra community, with *Juncus* and *Carex* inhabiting the wet surroundings during 14 050–13 400 cal. a BP (Figs 3 and 5; zones Nak-1, MA-1).

Table 2. Statistically significant local pollen assemblage zones (PAZ).

Local PAZ (depth in cm)	Age (cal. a BP)	PAZ description	Vegetation type
Nak-5 (1090–1050)	8 700–8 000	AP dominates up to 90%; *Alnus* appears, *Corylus* and *Pinus* expands	–
Nak-4 (1262–1090)	11 650–8 700	AP dominates up to 90%; *Betula* reaches 80%, *Ulmus* and *Corylus* appear, shrubs and NAP decline drastically. No corroded pollen is observed. PAR of AP rises to $>$20 000 grains cm^{-2} a^{-1}	Holocene forest expansion
Nak-3 (1464–1262)	12 850–11 650	AP/NAP ratio is roughly 50/50; tree types *Betula* and *Pinus* are less than 20%, shrubs *Betula nana*, *Salix* and *Juniperus* culminate. NAP is dominated by Cyperaceae, Poaceae, *Artemisia*, Chenopodiaceae, *Dryas octopetala* and *Helianthemum nummularium*. High relative abundance of corroded and inwashed pollen grains is observed. Most algae culminate at the upper limit of the PAZ. PAR of *Betula* is generally $<$1000 grains cm^{-2} a^{-1}	treeless herbaceous tundra
Nak-2 (1500–1464)	13 400–12 850	AP dominate up to 80%; *Betula* and *Pinus* reach over 30%, shrubs *Betula nana*, *Juniperus* expand. Green algae *Tetraedron* and *Botryococcus* flourish. Few corroded and inwashed pollen are observed. *Betula* PAR rise to 4700 and *Pinus* PAR increase to 2400 grains cm^{-2} a^{-1}	Forest-tundra with birch, scattered pine
Nak-1 (1656–1500)	14 050–13 400	AP/NAP ratio is 40/60; tree types *Betula* and *Pinus* are $<$20%, shrubs *Betula nana*, *Salix*, and *Juniperus* are present. NAP part is dominated by Cyperaceae, Poaceae, *Artemisia*, Chenopodiaceae and *Dryas octopetala*. High relative abundances of corroded and inwashed pollen grains are recorded. *Betula* PAR is $<$500 grains cm^{-2} a^{-1}	Treeless pioneer tundra

AP, arboreal pollen: NAP, non-arboreal pollen.

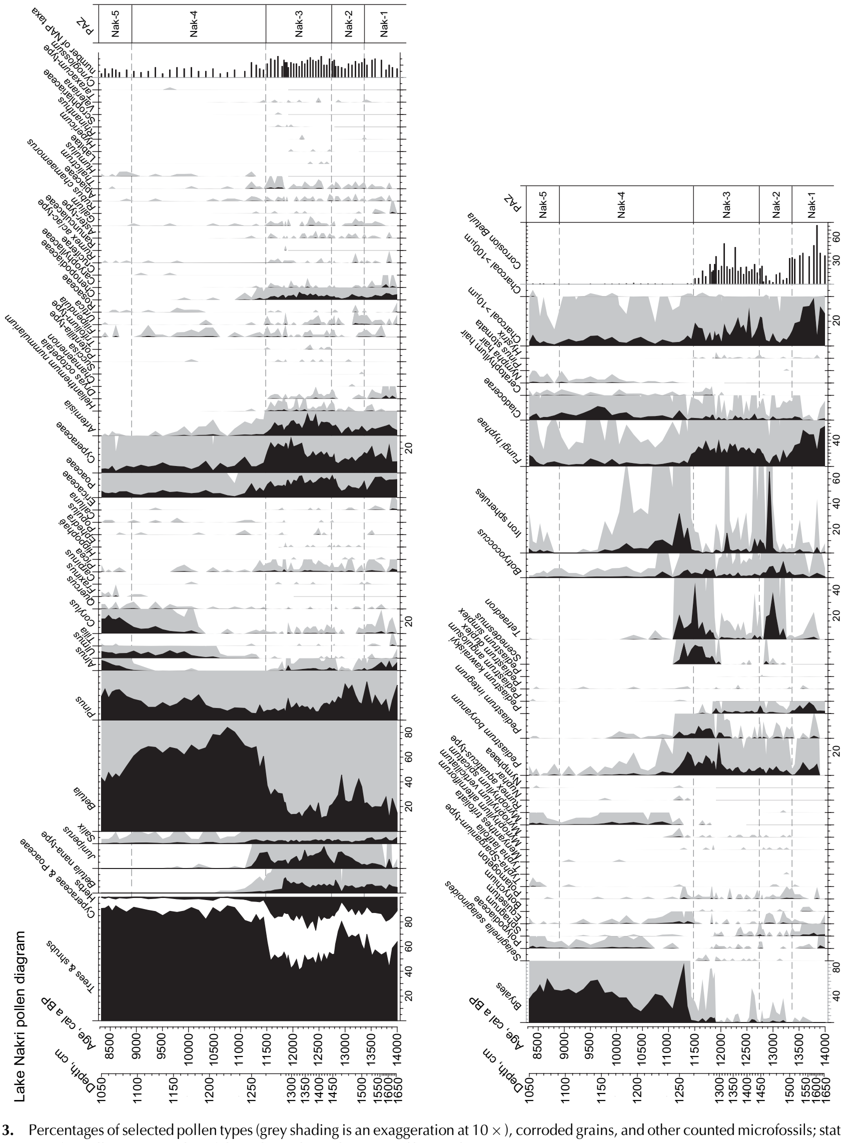

Figure 3. Percentages of selected pollen types (grey shading is an exaggeration at 10 ×), corroded grains, and other counted microfossils; statistically significant PAZ for pollen stratigraphy of the Lake Nakri sediment profile are shown.

The pollen found in the samples was highly corroded, indicating that 40–80% of birch pollen and 100% of alder and hazel pollen were inwashed from older sediments. These older sediments were probably from the Eemian flora, which were incorporated in the Late Weichselian tills surrounding the lake. The relative abundance of local birch and pine pollen throughout the Lateglacial period remained at around 20%, which contradicts the findings of earlier studies wherein pine reached values of over 80% (Pirrus, 1969, 1971; Pirrus and Raukas, 1996). Such high percentages of pine in earlier studies may indicate the enrichment of easily floating pine pollen in the heavy-liquid pollen-sample treatment process that was widely used in past years, or may be due to selective pollen counting of large pollen grains in poor-quality samples.

Considering the high corrosion index, we may subtract the supposedly inwashed portion of the tree pollen and thus obtain more accurate and even lower PARs for the dominant trees. Hyvärinen (1975, 1976) set 500 pollen grains cm^{-2} a^{-1} as the limit for the presence of pine, which was further developed by Hicks (2001) and Seppä and Hicks (2006) for other dominant

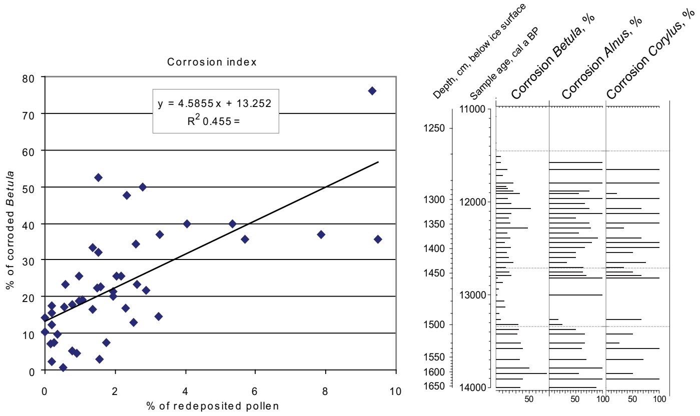

Figure 4. Corroded and degraded grains of *Betula*, *Alnus*, and *Corylus* pollen types. The goodness-of-fit (R^2) between the abundance data for inwashed thermophilous, i.e. re-deposited pollen, and corroded pollen was 0.463 (while that for *Betula* alone was 0.455).

arctic taxa, e.g. birch and spruce (500 and 50 pollen grains cm^{-2} a^{-1}, respectively). The PAR in Lake Nakri is very low; both *Betula* and *Pinus* PAR values are less than 500 grains cm^{-2} a^{-1} (Fig. 6). Thus the PAR values and species composition of Lake Nakri during 14 050–13 400 cal. a BP clearly indicate the presence of treeless tundra conditions in the area, which is supported by the lack of tree-type macro-remains. Presumably, the period when the ice sheet decayed from the area was too short to permit the immigration of trees to formerly ice-covered areas. In addition, the vicinity of the ice margin possibly influenced the migration rate of the tree line. The mean temperature of the warmest month at that time was below 11°C (Virtanen *et al.*, 2004), as judged for treeless conditions.

Evidence of local vegetation that was derived from macrofossil analysis supports the above conclusions that open tundra-type vegetation was present, based on findings of *Dryas* leaves and the seeds of dwarf shrubs. *Empetrum* has been reported to be one of the first woody plants to occupy newly formed landscapes after the glacial retreat in northeastern Greenland during the early Holocene (Bennike *et al.*, 1999). Early colonisers, such as *Saxifraga stellaris* and *Armeria*, are also adapted to severe environments. *S. stellaris* currently grows in Norway, Iceland, and Svalbard. *Armeria* sp. grows in Iceland and along the coasts of southern Scandinavia. This species is considered an indicator of sandy habitats and tolerates minimum mean January temperatures of as low as −8°C (Aalbersberg and Litt, 1998). In our study, the concentration of macrofossils was higher in the lowest part of the sequence MA-1 and became visibly lower between 13 750–13 500 cal. a BP (Fig. 5). This decrease may coincide with a cooler episode inside the GI-1c event, which was centred around 13 600 cal. a BP (Lowe *et al.*, 2008). However, no other data, except a slight decrease in LOI values, support this assumption.

13 400–12 850 cal. a BP: forest-tundra with birches and scattered pines

Clear signs of a 500-year long warming, which were mainly associated with the end of GI-1c and GI-1a warming event, appeared in all proxies of Lake Nakri. During 13 400–12 850 cal. a BP, the LOI of the sediment increased from 2%

Table 3. Lake Nakri plant macrofossil assemblages (MA).

MA (depth in cm)	Age (cal. a BP)	MA description
MA-5 (1256–1160)	11 350–9 800	Assemblage is characterised by (re)appearance of *Betula* sect. *Albae* and *Populus tremula* remains
MA-4 (1370–1256)	11 350–12 200	Species spectrum is dominated by cold-tolerating shrubs (e.g. *Betula nana, Salix polaris*) with variety of herbs (different grasses, *Saxifraga, Cirsium* etc.). *Dryas octopetala* reappears ca. 12 000 cal. a BP. Telmatic and aquatic species (*Carex* types, *Eleocharis, Juncus, Selaginella, Potamogeton filiformis*, Characeae) are present constantly. At the end of the zone a rise in amount of limnic organism remains (*Daphnia, Cristatella mucedo*) occurs. The species composition is similar to MA-3 but the abundance of macrofossils is higher
MA-3 (1473–1370)	13 000–12 200	Species composition consists of dwarf shrubs (*Betula nana, B. humilis*) and herbs (e.g. *Saxifraga, Rorippa*). Aquatic environment is characterised by one finding of *Potamogeton gramineus* and constant occurrence of Characeae oospores. *Plumatella* and *Cristatella* statoblasts are present in lower part of the zone. Abundance of macrofossils is relatively low
MA-2 (1515–1473)	13 450–13 000	Species spectra consist of trees (*Betula* sect. *Albae*), dwarf shrubs (*B. nana, Salix*) and telmatic/aquatic plants (*Eleocharis, Juncus, Selaginella,* Potamogetonaceae, Characeae etc.). Abundance of limnic animal remains (especially *Cristatella mucedo*) is highest. The first tree-type birch occurs at 1499 cm (ca. 13 400 cal. a BP)
MA-1 (1635–1515)	14 000–13 450	Lowermost 20 cm of the sediment is barren of plant macrofossils. The dominating plant species found are *Dryas octopetala* and *Betula nana*. The rest of the vegetation spectrum consists of grasses, Saxifragaceae and *Carex* types

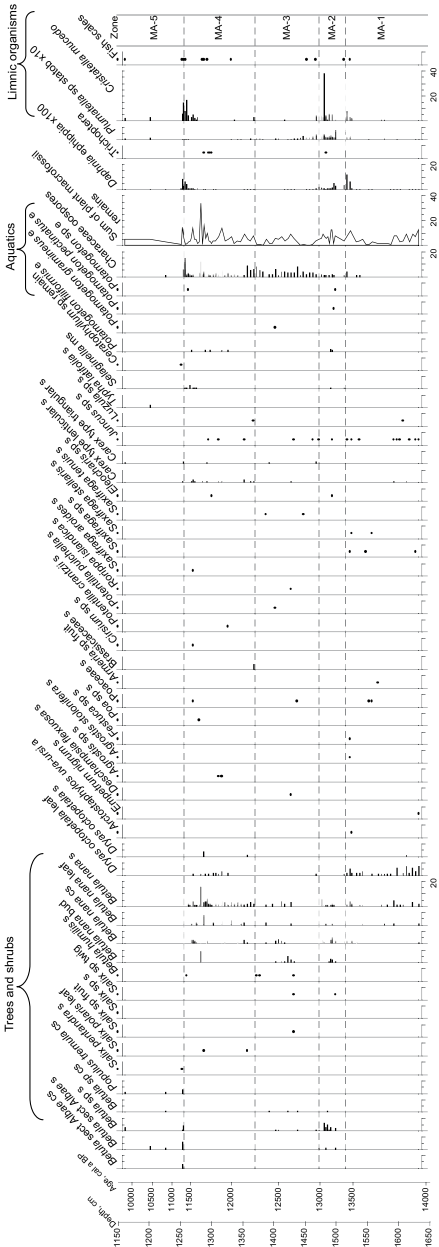

Figure 5. Number of plant macrofossil and limnic animal remains per 100 cm^3 of sediment from Lake Nakri. The species for which only a single specimen was found in a sample are presented using a presence/absence scale to increase the visibility of even one single seed. Key to abbreviations: s, seed; e, endocarp; a, anther; cs, catkin scale; ms, megaspore.

to 7.5% (Fig. 2), and the PAR value was considerably higher, especially tree pollen, and was accompanied by tree birch finds in the macrofossil evidence (Tables 2 and 3; zones Nak-2 and MA-2/MA-3, Fig. 6). The July mean temperature was estimated to be over 11°C, to support the presence of tree birch. Generally, this warming is regarded to encompass the whole of Allerød in the Baltic countries (Thomson, 1931; Pirrus, 1971; Kabailienė and Raukas, 1987; Kalnina, 2001). However, the present study shows that only the sediments from the later part of Allerød had high organic content, while the material deposited in the earlier part of Allerød was of minerogenic silt.

Hicks (2001) set the local birch forest limit at 1000 grains cm^{-2} a^{-1}. However, Birks (2003) warned that reconstructions based on pollen evidence should be validated by independent evidence of plant macrofossils. In the sections that were studied here, birch PAR reached over 4000 grains cm^{-2} a^{-1}, with a low proportion of corroded *Betula* pollen grains, which confirms that most of the birch pollen was local. The occurrence of *Betula* sect. *Albae* seeds confirm the local presence of tree birch. The corroborating evidence of both analyses for Nakri indicates the presence of birch forest during 13 400–12 850 cal. a BP. There was a subsequent rapid rate of colonisation, with the forest limit being surpassed in less than 50 years. McLachlan *et al.* (2005) suggested that glacial-age populations of temperate trees may have been located much farther north, i.e. closer to the ice margin, than suggested by pollen records or that recently shown by Heikkilä *et al.* (2009).

Pine PAR values surpassed the local presence limit of 500 grains cm^{-2} a^{-1} (Hicks, 2001) between 13 300 and 12 850 cal. a BP, and the forest limit of 1500 grains cm^{-2} a^{-1} between 13 150 and 12 850 cal. a BP. Thus far, there is no evidence of Lateglacial pine macrofossils from Estonia. However, a find of a single *Pinus* stoma in 13 300 cal. a BP at Nakri (Fig. 6) supports local presence of pine during the Lateglacial. Evidence of modern pine stomata at the Kola Peninsula suggests that stomata were present only in forest and pine forest tundra with pine PARs of over 500 grains cm^{-2} a^{-1}, and in *Pinus* pollen with a relative abundance of over 35% (Gervais and MacDonald, 2001; Gervais *et al.*, 2002). Pine distribution and growth are generally regarded to be highly dependent on summer temperature (Seppä *et al.*, 2008). The critical mean July temperature limits for the flowering of *Pinus* and *Picea* are 12°C and 13°C, respectively, depending on the ecological range of the mentioned taxa, and is 13°C for *Betula* (Huusko and Hicks, 2009; Kuoppamaa *et al.*, 2009). As tree birch is present in the area surrounding Lake Nakri, and its critical flowering limit is higher than or equal to that of pine and spruce in modern times, the latter two taxa may have been represented in the vegetation. However, Paus (1995) argues that the presence of birch in more continental areas such as Nakri may exceed the temperature limit of the warmest month, instead correlating with the mean maximum July temperature. Velichko *et al.* (2002) modelled the Lateglacial July mean temperature of northeastern Russia to be about 3–3.5°C colder than today, which would be 13–13.5°C. The closest strong evidence of pine and spruce in Allerød flora comes from about 180 km southeast of Lake Nakri, where Lateglacial sediments of Lake Kurjanovas in Latvia yielded *Pinus* and *Picea* bud scales (Heikkilä *et al.*, 2009). However, *Pinus* pollen percentages at this location were double those observed at Lake Nakri.

The warmer climate during 13 400–12 850 cal. a BP not only favoured the terrestrial vegetation but also nourished aquatic life such as pondweeds (*Potamogeton* genus), e.g. *P. pectinatus* and *P. filiformis*, and Characeae oospores as well as green algae *Pediastrum*, *Scenedesmus*, *Tetraedron minimum*, and *Botryococcus*. Ralska-Jasiewiczowa *et al.* (2003) reported that major blooms of *Tetraedron* were synchronous with major increases

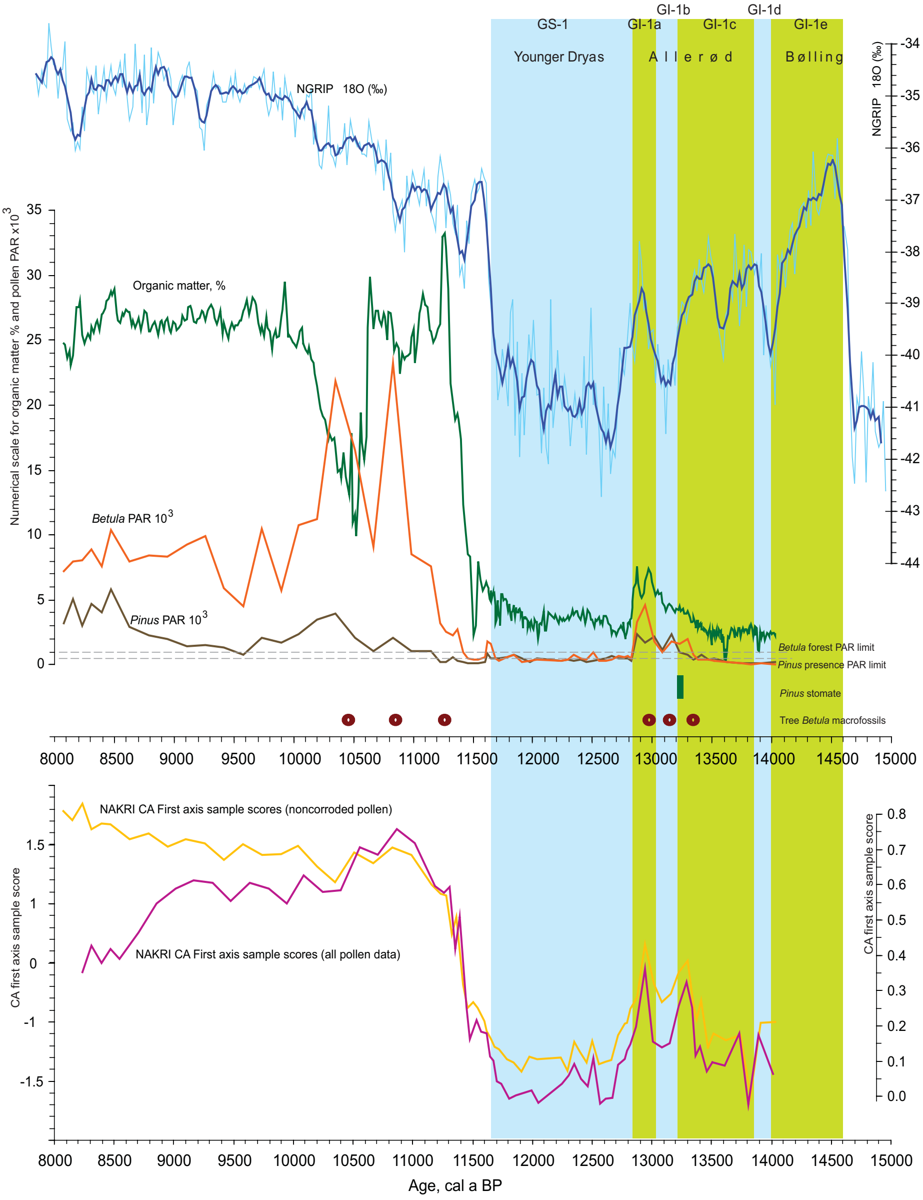

Figure 6. Summary graphs from Lake Nakri compared to Greenland NGRIP δ^{18}O (‰) data (Rasmussen *et al.*, 2006). PARs of tree taxa *Betula* (lines for all birch pollen in blue and non-corroded in orange) and *Pinus* show an increase in the latter half of the Allerød, and a decrease during the cold reversal GI-1b. High tree PARs are associated with finds of tree macrofossils (marked as dots). The CA first axis sample scores of the Lake Nakri pollen data summarise the amount of compositional change between adjacent samples, primarily reflecting the climatic signal; more positive values indicate higher temperature. This figure is available in colour online at wileyonlinelibrary.com.

in δ^{18}O in Lake Gościaz within a matter of years, thus indicating warming. *Pediastrum kawraiskyi* and *Botryococcus* were clearly pioneering species that preferred colder climates and oligotrophic conditions, which are the opposite of conditions preferred by other green algae (Barrientos, 1979; Veski, 1994; Jankovská and Komárek, 2000; Sarmaja-Korjonen *et al.*, 2006; Weckström *et al.*, 2009).

Many plant species act as environmental indicators, while limnic animals have also been used for palaeoclimatological estimations (Lotter *et al.*, 1997; Duigan and Birks, 2000).

Limnic bryozoan species found in macrofossil samples have a well-studied ecology in Nordic environments (Økland and Økland, 2000, 2005). Bryozoans (*Cristatella mucedo*, *Plumatella* sp.) grow mostly during the ice-free periods of the year. Thus larger concentrations of limnic animals coincide with longer open-water seasons (Väliranta *et al.*, 2006). Based on ecological studies, *Cristatella mucedo* occurs in open large bodies of water, e.g. lakes, which have poor or medium aquatic macro-vegetation. In addition, this species is sensitive to water temperature (occurs in summer water temperatures of >6°C, but strongly prefers temperatures of >16°C; Økland and Økland, 2000). The cladoceran *Daphnia* sp. is reported to be an immediate Lateglacial pioneer taxon in Norway, albeit in small numbers; *Daphnia* sp. ephippias were especially abundant during the 'Allerød warming' and the Holocene, but were absent in the cooler Younger Dryas (Duigan and Birks, 2000; Bennike *et al.*, 2004). In the Lake Nakri record, the first clear increase in the concentration of *Cristatella mucedo* statoblasts coincided with increases in *Daphnia* sp. ephippia and *Plumatella* sp. statoblasts during the GI-1a event. These changes occurred at approximately the same time period as the first appearances of *Betula* sect. *Albae* (tree birch) and *Potamogeton pectinatus*, indicating that milder climatic conditions existed.

Within the ca. 500-year-long warming period, a short cooling event, which was associated with the GI-1a and 1c warming events, was possibly detected. This was evident mainly through a decrease in birch and pine PAR values centred at 13 100 cal. a BP and connected with the GI-1b cooling, which has been recognised as the Gerzensee fluctuation in western European records (Lotter *et al.*, 1992). The pollen count percentages from Lake Nakri provide evidence that a similar birch and pine pollen reversal occurred in comparison to that observed in high-resolution Danish (Andresen *et al.*, 2000), northeast German (de Klerk, 2008) and Norwegian (Karlsen, 2009) Lateglacial sediment records.

12 850–11 650 cal. a BP: treeless herbaceous tundra

In 12 850 cal. a BP and the start of the Younger Dryas (GS-1) cooling event, the vegetation in southern Estonia again became dominated by herbs and dwarf shrubs (Table 2, zone Nak-3). The corrosion index (Fig. 4) also indicated the higher input of inwashed pollen and lower local tree pollen production. *Artemisia*, *Dryas*, *Helianthemum*, *Juniperus,* and *Betula nana* dominated the pollen record, and the macrofossil evidence showed a high concentration of dwarf birch and *Dryas octopetala*. Tree birch macro-remains disappeared. The occurrence of botanical macro-remains of species adapted to the arctic climate, such as *Potentilla pulchella*, *Rorippa islandica*, *Saxifraga tenuis*, *Salix polaris*, *Betula humilis*, and *Potamogeton gramineus*, were noted, indicating cooler climate conditions with a minimum mean July temperature of 8°C (Gaillard and Birks, 2007). Macrofossils were very rare around 12 850–12 700 cal. a BP, which is associated with the coldest period of GS-1 (Lotter *et al.*, 2000; Ilyashuk *et al.*, 2009). The occurrence of different Poaceae, Saxifragaceae and other dry habitat species (*Potentilla pulchella*, *P. crantzii*) indicates the presence of dryer environmental conditions. *Rorippa islandica* has been reported as an arctic drought-tolerant pioneer species from Karelia during 11 800 cal. a BP (Wohlfarth *et al.*, 2002).

PAR values of *Betula* and *Pinus*, especially without the degraded proportion, remained below the presence limit of these taxa. Forests persisted in eastern Latvia throughout the Younger Dryas, as indicated by macrofossil finds of birch, pine, and spruce (Heikkilä *et al.*, 2009). The high relative abundance of spruce pollen at Lake Päidre in southern Estonia (Saarse *et al.*, 1995), and a find of undated spruce wood from sediments (Thomson, 1934), may imply its sporadic presence in Estonia but not in the vicinity of Lake Nakri.

The absence of pine and tree birch suggests that summer temperatures were below 12°C. The mean July temperature estimates for the Younger Dryas inferred from pollen and chironomid from northwestern Europe suggests that temperatures were 4.5°C lower than at present (Seppä *et al.*, 2002), and 1.5°C colder than during the Allerød (Lotter *et al.*, 2000). Temperatures were around 13°C during the coldest part of the Younger Dryas (Heiri *et al.*, 2007). Renssen and Isarin (2001) reported that minimum July temperatures were ~10°C in southern Estonia, which corroborates the approximately 2°C summer temperature drop at the Allerød/Younger Dryas boundary (Brooks and Birks, 2001; Heiri *et al.*, 2007).

11 650–9000 cal. a BP: Holocene forest expansion

Gyttja sedimentation gradually began in 11 650 cal. a BP during the Lateglacial/Holocene boundary. Within 300 years, the organic content reached over 25%. The varved section of the gyttja sediments (unit 5 in the lithostratigraphy) indicated relatively deep water with an anoxic hypolimnion. The vegetation response for climate change at the Younger Dryas/Holocene consisted of rapid forestation and the loss of the Lateglacial floristic component (Table 2, PAZ Nak-4). Successions of *Populus*, *Ulmus*, *Corylus,* and *Alnus* into the birch–pine forest define the early Holocene forest composition, of which *Betula* sect. *Albae* and *Populus tremula* were also recorded in the macrofossil data. The latter is not represented well in the pollen evidence. Therefore, the pollen and macrofossil indicators supplement one another. The increase in the concentration of tree birch macro-remains, which was accompanied by the appearance of aspen (*Populus tremula*), *Salix pentandra*, and the wetland/water plants *Typha latifolia* and *Ceratophyllum* sp., suggest that the minimum mean July temperature was around 13°C (Isarin and Bohncke, 1999).

Lateglacial Vegetation dynamics on a regional scale

Lateglacial environmental conditions in the eastern Baltic area have gained attention in recent years as a result of several detailed multiproxy studies being carried out in locations of the Baltic and western Russia to refine knowledge about the retreat of the SIS. The current dataset, which addresses the Lateglacial period in Estonia, fills the spatial gap from the already published study sites of Lithuania, Latvia, and western Russia.

At the southern end of the eastern Baltic area in Lithuania, the latest studies on Lateglacial vegetation change have placed the appearance of pioneer vegetation at the GI-1e phase in western Lithuania (Stancikaite *et al.*, 2008). In southeast Lithuania, the Lateglacial vegetation record began in 14 300 cal. a BP with tundra-like vegetation, but macro-remains of tree birch and pine were already present, showing more of a forest-tundra characteristic. This community was then succeeded by birch (both dwarf and tree birch) and pine forests, which again became more open habitat during the final cooler part of the Lateglacial period from 12 600 cal. a BP until the onset of the Holocene (Stancikaite *et al.*, 2008). Further north, in eastern Latvia, the start of postglacial vegetation is placed at more than 16 000 cal. a BP, and began with a tundra community that rapidly changed to dense pine forest, with some tree birch being present in 14 400 cal. a BP. During the Younger Dryas, the forest was reduced in favour of shrubs and herbaceous taxa, with the first occurrence of spruce (Heikkilä *et al.*, 2009).

The general pattern of transition from the tundra community to the birch–pine forest, with a subsequent forest decline during the Younger Dryas cooling, is also evident in Estonia, but it is observed more clearly in pollen PAR data than in plant macrofossils. In southern Estonia, during 14 000–13 400 cal. a BP treeless pioneer tundra vegetation prevailed, and during 13 400–12 850 cal. a BP birch and pine forests spread across the area. The GI-1b (Gerzensee) cooling in 13 100 cal. a BP affected the vegetation. In fact, a clear sign of warming in the sediments of Lake Nakri was seen at GI-1a, when there was a decline of cold-tolerant plant macrofossils in favour of more temperate species. Mostly treeless vegetation spread again during 12 850–11 650 cal. a BP.

The finds of tree macrofossils that would validate the presence of species on a local scale are scarce (Fig. 6). It is surprising that none of the study sites that were analysed for plant macrofossils in Estonia contained coniferous tree macro-remains in the Lateglacial period, except for a single pine stoma (Fig. 6). The only type of tree species that was confirmed by the macrofossils until the Holocene was tree birch (*Betula* sect. *Albae*). In Lithuania, the presence of tree birch macrofossils was reported from 14 300 cal. a BP onwards (Stancikaite *et al.*, 2008). In northeast European Russia, tree birch macrofossils date back to 12 800 cal. a BP (Väliranta *et al.*, 2006). In west-central Russia, tree birch macrofossils were found in sediment dating from 10 600 cal. a BP, although birch pollen was present several thousand years earlier, at approximately 14 000 cal. a BP (Wohlfarth *et al.*, 2006). In southern Estonian localities, Solova (Amon *et al.*, 2010) and Nakri, tree birch was found around 13 500–13 400 cal. a BP. In comparison with the spatially closest study site in Latvia (Fig. 1), the time lag for tree birch to migrate from central Latvia to southern Estonia was approximately 1000 years, based on macrofossil evidence. Colonisation was probably inhibited by unfavourable environmental conditions within the proximity of the ice edge of the SIS.

In northern Estonia, no tree macro-remains were found, and a shrub–herbaceous vegetation community dominated throughout the Lateglacial period (Amon and Saarse, 2010). The gradual vegetation succession from tundra to forest, and the reintroduction of grasslands during the Younger Dryas in the Baltic area, was also independently demonstrated by mammoth migration paths to seize the tundra-steppe communities in the Lateglacial period (Ukkonen *et al.*, 2011). A similar absence of coniferous macro-remains and the presence of tree birch in the Holocene only were also found in Karelia, which is northeast of Estonia (Wohlfarth *et al.*, 2002). Pollen data from the Karelian Isthmus (Fig. 1) show a pattern of tundra pioneer vegetation that formed in ca. 13 000 cal. a BP, changing into pine–birch–spruce forest as late as 11 000 cal. a BP (Subetto *et al.*, 2002).

Estonian Lateglacial vegetation dynamics seem to be more similar to that of Karelia when compared with the vegetation development in spatially closer eastern Latvia, revealing a circum-ice-edge pattern of vegetation succession and indicating a clear zonation of vegetation in front of the declining ice sheet. The reconstructed dry climatic conditions, gradual melting of ice and permafrost, long-lasting lake-ice cover, and erosion from unstable soils are characteristic of study sites in Karelia and in Estonia. These parameters result in vegetation succession being a prolonged process (Wohlfarth *et al.*, 2007). The proximity of the retreating ice and the cold waters of the large proglacial lakes that developed in front of the retreating ice margin may also have inhibited vegetation development in Estonia, causing unfavourable environmental conditions for warmth-demanding species, and suppressing the spread of tree species from Latvia.

Conclusions

This paper presents detailed Lateglacial and early Holocene vegetation succession in southern Estonia during 14 000–9000 cal. a BP. Palaeoecological analyses of the sediment core from Lake Nakri, southern Estonia, have provided important insights into the understanding of timing, vegetation dynamics, and changes in palaeoenvironmental conditions during the Lateglacial period in the eastern Baltic area. The current study is based on pollen analysis, including PAR, plant macrofossils, and the content of organic matter. A chronology of the sediment core was established on the basis of nine AMS ^{14}C dates of terrestrial macrofossils, and suggests the onset of sediment accumulation ca. 14 000 cal. a BP. Biostratigraphic evidence indicates treeless pioneer tundra with dwarf shrubs and arctic species, and hence a cold climate in southern Estonia ca. 14 000–13 400 cal. a BP. Tree birch macro-remains and high *Betula* PAR imply the presence of forest-tundra with birch in 13 400–12 850 cal. a BP, with the rapid colonisation and development of forested areas in response to climate improvement since the GI-1c. Macrofossil and PAR evidence show that the climate was warmest in 13 000–12 850 cal. a BP, which was associated with the GI-1a. There are no indications of conifer macrofossils in Estonia to support coniferous forests in the Lateglacial period. However, the find of a single *Pinus* stoma and high PAR of pine suggest the local presence of pine as sporadic isolated patches. The GI-1b cooling in 13 100 cal. a BP is evident in the Lake Nakri sediment record. Our data show that during 12 850–11 650 cal. a BP the tree species declined, and treeless herbaceous tundra vegetation developed, followed by forest expansion in response to rapid Holocene climatic warming.

The vegetation development was clearly affected by climatic conditions; the unity of studied palaeobotanical assemblage zones and regionally synchronised palaeoclimatological events is notable. Comparison of Lateglacial vegetation dynamics at a regional scale suggests the formation of vegetation zones that are more related to the proximity of the retreating ice sheet than actual latitude.

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Abbreviations. AMS, accelerator mass spectrometry; AP, arboreal pollen; CA, correspondence analysis; GI, Greenland Interstadial; GS, Greenland Stadial; LOI, loss-on-ignition; NAP, non-arboreal pollen; PAR, pollen accumulation rate; PAZ, pollen assemblage zones; SIS, Scandinavian Ice Sheet.

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PAPER IV

Veski S., Amon L., Heinsalu A., Saarse L. and Vassiljev J.
Late-Glacial vegetation dynamics in the eastern Baltic region,
a complete record since the Bølling (GI-1e) (manuscript).

Late-Glacial vegetation dynamics in the eastern Baltic region, a complete record since the Bølling (GI-1e)

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Abstract

This paper discusses a complete record of vegetation history since the Bølling (GI-1e) warming (14 500 cal yr BP) up to the Holocene. To date, this is the only complete record of such age in the eastern Baltic area and the northernmost area for which Bølling records are present. Combining pollen evidence, accumulation rates and plant macrofossil data, we assess the local and regional vegetation development, and we attempt to separate the true Late-Glacial vegetation signal by removing the obviously redeposited termophilous pollen; however, we remove not only their signal, we discuss the possibilities of separating the redeposition signal of the so-called "local Late-Glacial trees", pine and birch, by looking at their corrosion and degradation. The results show that the Bølling warming in the eastern Baltic area was a treeless tundra community consisting of the shrubs *Betula nana, Dryas octopetala* and *Salix polaris*. The Older Dryas cold spell is clearly recognised as a decline in the total concentration of plant macrofossils and pollen accumulation rates (PARs) at between 14 200–13 500 cal yr BP. At 13 460 cal yr BP, the *Betula nana* macrofossils disappear, and tree-birch (*Betula* sect. *Albae*) appears, marking the start of tree birch forest as the *Betula* PAR reach over 2000 grains cm^{-2} yr^{-1} as well as *Pinus* PAR. The presence of pine forest is confirmed by a variety of macrofossils, including bark, wood, needles and seeds, since 13 400 cal yr BP, at the same time at which pine stomata are found. The first identified pine stomata finds are associated with a *Pinus* PAR over 3000 and pine macrofossil finds with a *Pinus* PAR over 4000 grains cm^{-2} yr^{-1}. During the warmest period of the GI-1a (Allerød) warming at 13 000–12 700 cal yr BP, a pine forest with deciduous trees (birch – *Betula pendula* and aspen – *Populus tremula*) developed in the Baltic region. The Younger Dryas (GS-1) cooling strongly affected the floral composition in eastern Latvia, and the forest species declined abruptly from a maximum PAR at 12 700 to a PAR below 1000 grains cm^{-2} yr^{-1} at 12 600 cal yr BP, i.e., the response time for the pine forest to collapse was 100 years according to the PAR data. Pine macrofossils disappear simultaneously with the pollen signal at 12 600 cal yr BP, yet occasional *Pinus* stomata are recorded throughout the Younger Dryas (GS-1). The landscape was treeless shrub tundra again, with *Dryas octopetala, Salix polaris, B. nana* and *Juniperus* present.

Picea is introduced in the region within the cold Younger Dryas and is represented by stomata (12 400–12 200 cal yr BP), needles, seeds and wood (since 12 050 cal yr BP up to the Holocene). The Pleistocene/Holocene boundary at 11 650 cal yr BP is marked by changes both in vegetation composition and sediment type. The organic rich gyttja accumulated instead of silts and clays, and the start of the Holocene warm period permitted forest re-expansion in eastern Latvia.

Keywords: Late-Glacial vegetation; pollen; plant macrofossils; corrosion index; deglaciation; Latvia.

1. Introduction

Understanding the long-term dynamics of ecosystems is critical to predicting their response to future environmental changes. The post-glacial environmental and climatic change with abrupt cooling, which interrupted the general warming trend as new land surfaced from under the ice cap of the last glaciation, has been studied for approximately a hundred years (Hartz and Milthers, 1901; Andersson, 1909; Hausen, 1913). These studies have revealed changes and rates of changes in Earth's climatic system as well as locations of plant refugia, vegetation recolonisation routes and speeds (e.g., Bennett et al., 1991; Tarasov et al., 1999, 2000; Ravazzi, 2002; Ohlemüller et al., 2011). Palaeoecological records preserved in sedimentary deposits can provide unique insight into the nature of past ecosystems and the long-term plant population and plant community dynamics. Alongside the traditional Quaternary geological methods in investigating the glacial refugia and recolonisation, molecular tools (Taberlet et al., 1998; Sinclair et al., 1999; Hewitt, 2000; Petit et al., 2003; Cottrell et al., 2005) are applied to more precisely locate the flora asylums and regeneration from them. New evidence of Late-Glacial (LG) habitat mammals, such as the woolly mammoth and the reindeer, moving together with the receding ice front and the open tundra strip, gives independent flora/community background to these areas (Ukkonen et al., 2006, 2011). The concept of treeless tundra in the eastern Baltic region fails to explain the rapidity of the LG and postglacial tree population dynamics of the region, showing that tree populations were present there at times (Heikkilä et al., 2009) and vanishing at others. Abrupt LG reversing climate change events occurred over the span of decades, such as in the Younger Dryas 12 850–11 650 cal yr BP (Lowe et al., 2008), when the cooling average summer temperatures dropped by approximately 3–4 °C, followed by a 7 °C warming in just 20–50 yr based on Greenland data (Dansgaard et al., 1989; Alley et al., 1993). Such reversals influenced the postglacial succession of flora and fauna (e.g., Litt and Stebich, 1999; Birks and Ammann, 2000; Lotter et al., 2000; Lõugas et al., 2002; Birks and Birks, 2004; Mortensen et al., 2011).

LG studies in the eastern Baltic area span over a century, focusing on ice-recession lines and chronology (Kalm, 2006). In recent years, new data on ice retreat involve varvochronology (Sandgren et al., 1997; Hang, 2003), new dating methods (Rinterknecht et al., 2006, 2008), reviews (Raukas et al., 2004; Kalm et al., 2011) and palaeobotanical data (Saarse et al., 2009; Amon et al., 2010, 2011; Amon and Saarse, 2010; Kihno et al., 2011).

This paper discusses a complete record of vegetation history since the Bølling warming (14 500 cal yr BP) up to the Holocene and is thus far the only record of this age in the NE Baltic area and the northernmost area where Bølling records are available. We combine pollen evidence, pollen accumulation rate (PAR) and plant macrofossil data to assess the local and regional vegetation development. We also attempt to separate the true LG vegetation signal by removing the obviously redeposited termophilous pollen, but not just their signal; we also discuss the possibility of separating the redeposition signal of the so-called local LG trees pine and birch by looking at their corrosion and degradation, which will perhaps help us understand more precisely the LG vegetation in the eastern Baltic and elsewhere.

2. Study area

Lake Lielais Svētiņu (LS) is located in eastern Latvia, Rezekne district (56°45.5 N; 27°08.8 E), in the Lubana depression between the Latgale and Vidzeme uplands (Fig. 1). The area of the lake is 18.8 ha, the altitude is 96.2 m above sea level (a.s.l.), the mean depth is 2.9 m and the maximum depth is 4.9 m. The oblong brown-water humic water body belongs to the Daugava watershed area and has small inlets and outlets. The topography around the lake undulates, reaching up to approximately 100 m a.s.l., and the slope angle to lakeshore is low. The highest estimated LG shoreline in the area is 108 m a.s.l. The Quaternary cover consists mainly of silts and clays of the Lubana basin, which have been greatly paludified in the Holocene. Forested areas (birch forest) and a few farms surround the lake today.

3. Methods

3.1. Coring and lithostratigraphy

The sediment was cored from lake ice using a 10-cm-diameter Russian corer in March 2009. The water depth below ice was 4 m. The sediment thickness reached 11.35 m (of which the LG portion was the lowermost 3.75 m). In the present article, we used sample depths from the ice/water surface. Multiple parallel overlapping sediment cores were described in the field, photographed, carefully packed into 1-m plastic semi-tubes, wrapped in polyethylene film, labelled and

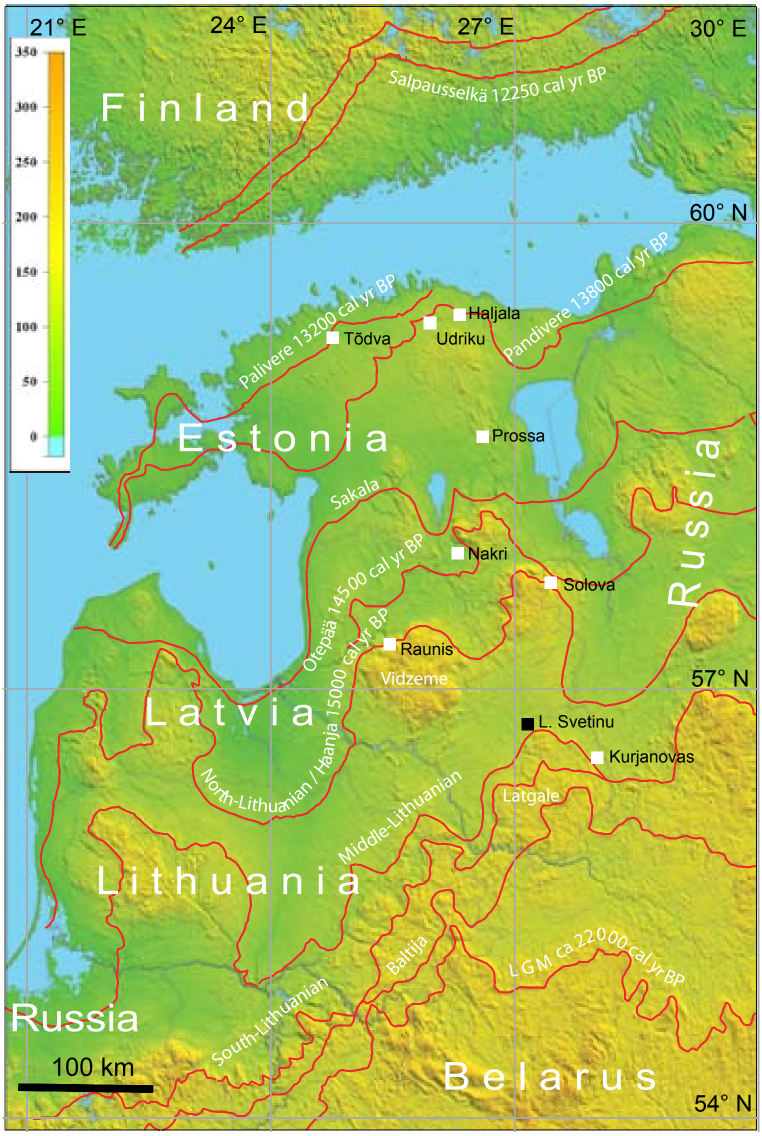

Figure 1. Schematic map of the Baltic region showing the Late-Glacial sites discussed in the text with the location of the Scandinavian Ice Sheet ice marginal zones (compiled from Kalm, 2006; Kalm et al., 2011). Ages of the ice marginal zones are from Saarnisto and Saarinen (2001), Saarse et al. (2011), Amon and Saarse (2010), Kihno et al. (2011) and Kalm et al. (2011).

transported to the laboratory for further analyses. The LG interval of the sediment core was analysed for the present study. The Holocene sediment was transported to Latvian University for additional analyses. The organic matter (OM) content of the sediment was determined by loss-on-ignition at 550 °C for 4 h (Heiri et al., 2001). The magnetic susceptibility (MS) was measured with a Bartington MS2E meter (Nowaczyk, 2001).

3.2. Palaeobotanical methods

The preparation for plant macrofossil analysis followed conventional procedures (Birks, 2001). The cores were sliced into 5-cm-thick intervals, and all material remaining after other analyses was used for plant macrofossil analysis. The sub-samples were determined by water displacement in a measuring cylinder. The sample size varied from 90 to 730 cm^3. The samples were wet-sieved through a 0.16 mm mesh. Material retained on the sieves was examined using a stereo and light microscope. The plant macrofossils were identified according to the relevant literature (Berggren, 1969; Anderberg, 1994; Cappers et al., 2006) and a reference collection. The counts were recalculated to a concentration (plant macrofossils per 1 cm^3). Seeds of tree-type birch (*Betula pendula* and *B. pubescens*) were grouped as *Betula* sect. *Albae*, and *Carex* seeds were divided into two groups by seed morphology: triangular seeds and lenticular seeds.

The pollen sample preparation followed a standard acetolysis method (Berglund and Ralska-Jasiewiczowa, 1986) combined with a cold concentrated 40% HF treatment followed by a hot concentrated 70% HF treatment to remove inorganic matter (Bennett and Willis, 2001). *Lycopodium* spores were added to calculate pollen concentration and, subsequently, the PAR values (Stockmarr, 1971). A pollen sum of at least 500 grains was obtained. The pollen data were expressed as percentages of the total terrestrial pollen sum, and the PAR values were expressed as pollen grains cm^{-2} yr^{-1}. Counts of spores, green algae, charcoal, and other microfossils were calculated as percentages of the total sum of terrestrial pollen. The *Betula nana*-type was differentiated from *Betula* on the basis of size and morphology (Mäkela, 1996; Caseldine, 2001). Corroded and degraded grains of *Betula* were counted separately during routine pollen analysis and used as a measure of redeposition or inwash from older sediments (Birks, 1970). These grains were compared with the ratio of *Betula* versus *Betula nana*-type pollen. Intact (unbroken) *Pinus* pollen grains were counted separately from the 'one air-sacked' or broken grains (two air-sacks count as one *Pinus* pollen grain), and the relationship of pine versus broken pine pollen was used as a measure of pine redeposition.

For diatom analysis, freeze-dried, weighted sediment sub-samples were digested in 30% H_2O_2 until the organic material was oxidised. A few drops of 10% HCl were added to remove carbonates, and thereafter, the fine mineral particles were removed by repeated decantation. Divinylbenzene microscopic markers were added to determine diatom concentration. A few drops of the cleaned sub-sample were dried onto the cover glass and mounted onto slides using a Naphrax medium

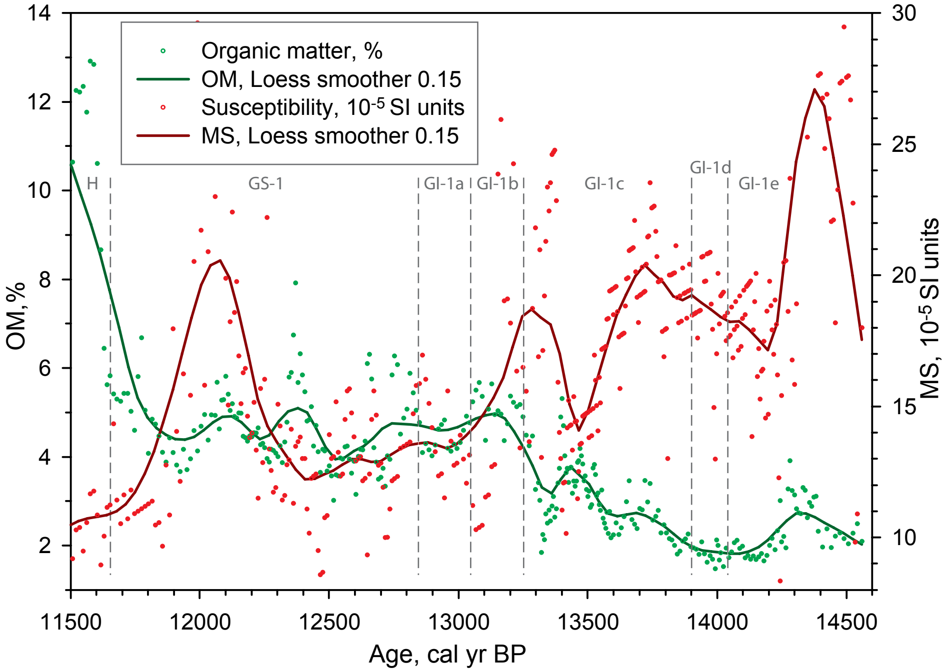

Figure 2. Organic matter (OM) content and magnetic susceptibility (MS) variability for Lake Lielais Svētiņu sediments.

and were analysed for microfossils under an Axio Imager light microscope at ×1000 magnification using oil immersion and differential interference contrast optics. The diatoms were identified using standard floras, and they were grouped according to their habitat into planktonic and periphytic taxa, the latter including epipelic, epipsammic and epiphytic life forms.

3.3. Chronology

Several samples containing material suitable for radiocarbon dating were selected and packed separately directly in the field, while most of the dating material was identified after sediment sieving in laboratory. Only terrestrial plant macrofossils were chosen as suitable material for radiocarbon dating, including twigs, bark, wood and seeds. The identified and cleaned specimens were sent to the Poznan Radiocarbon Laboratory, Poland. In total, 12 horizons were dated. The dates were calibrated, and an age–depth model was built with an OxCal 4.1 depositional model, including visible sedimentary boundaries (Bronk Ramsey, 2001; Reimer et al*.,* 2004).

3.4. Statistical methods

Pollen diagrams and macrofossil data were compiled using Tilia 1.0.1 (Grimm, 2007). The zonation of pollen and plant macrofossils was based on the binary splitting of the sum-of-squares method using the PSIMPOLL 4.10 programme (Bennett, 2002). The significance of statistically determined zones was estimated by comparison with the broken-stick model described by Bennett (1996). Macrofossil zonation using PSIMPOLL is based on macrofossil data for vascular terrestrial plants.

4. Results

4.1. Lithostratigraphy and chronology

The LG to early Holocene sediments from Lake LS were divided into 8 lithostratigraphical units (Table 1). The LG sediments consisted of sand, silt and laminated or varved clay. Several intervals contained dark, probably dispersed OM. The maximum OM content in the LG sediments was 7.9% at a depth of 1227 cm. Increasingly OM-rich gyttja started to accumulate in the early Holocene. The MS data have three periods of increased values: in the basal layers, in the mid-Allerød and in the Younger Dryas (Fig. 2, Table 1).

The chronology is based on 11 radiocarbon age estimations of terrestrial plant macrofossils (Table 2). By extrapolating the acquired age determinations to the

Table 1. Lithostratigraphy of Lake Lielais Svētiņu Late-Glacial and early Holocene sediments

Depth from water surface, cm	Age, cal yr BP	Sediment description	OM content, %	MS values, 10^{-5} SI units
1105–1160	11 650–10 910	Silty gyttja, greenish brown, homogeneous	4.2–13.6%	1.5–11.8
1160–1190	12 060–11 650	Silt, dark gray, with OM	3.7–6.9%	9.6–29.6
1190–1268	12 730–12 060	Silt, light gray	3.0–7.9%	8.6–30.7
1268–1317	13 310–12 730	Silt, yellowish, with OM	3.3–6.3%	10.0–25.9
1317–1332	13 400–13 310	Clay, distinctly laminated (varved clay?), about 20 lamina couplets	1.8–3.7%	13.0–24.8
1332–1498	14 250–13 400	Silt, gray, increasingly dark coloured from OM towards the upper limit	1.5–5.3%	8.3–23.5
1498–1515	14 390–14 250	Sand, dark coloured	1.9–3.2%	15.4–39.4
1515–1535	14 560–14 390	Sand, beige, compact	1.9–2.5%	6.0–29.5

Table 2. Radiocarbon ages of Lake Lielais Svētiņu sediment core. The weighted average ages of the deposition model in OxCal 4.1. (Bronk Ramsey, 2001; Reimer et al*.,* 2004) in column 5 were used in the age–depth model.

Depth, cm	Laboratory code	^{14}C date, yr BP	Calibrated age, cal yr BP, 2σ	Model age, cal yr BP	Material dated
1157	Poz-30426	10 100±60	11 650–11 590	11 620±20	Wood
1185	Poz-36710	10 270±50	12 140–11 810	11 990±90	Twigs
1215	Poz-31768	10 330±50	12 400–12 120	12 290±80	Wood
1261	Poz-31769	10 760±50	12 760–12 560	12 660±50	Twigs, bark
1315	Poz-36711	11 460±60	13 400–13 160	13 290±60	Bark
1355	Poz-36712	11 670±60	13 620–13 400	13 510±50	Stems
1365	Poz-36715	11 630±60	13 660–13 460	13 560±50	Twigs, *B. nana* leaves, *Potentilla* seed
1400	Poz-36713	11 840±60	13 830–13 640	13 740±50	Twigs
1445	Poz-36714	12 410±60	14 240–13 990	14 110±60	Twigs, *B. nana* leaf (rejected from model)
1492	Poz-31770	12 380±60	14 440–14 040	14 220±100	Twigs, bark
1510	Poz-29298	12 420±60	14 590–14 150	14 350±110	Wooden material
1530	Poz-31771	12 350±60	14 950–14 180	14 520±210	Wooden material

basal part of the sediment record, we estimated the start of sedimentation in Lake LS at 14 560 cal yr BP. The model shows a poor agreement index (A=40) at the 1445 cm level, and the dating was rejected on the basis of that value.

In addition to establishing the chronology for the LG sediment interval of Lake LS, eight bulk samples on Holocene gyttja were also dated by the conventional method at the TTU Institute of Geology (not shown here).

4.2. Fossil pollen record

The LG pollen record of Lake LS comprised 48 sample levels and 88 microfossil types, which were divided into 7 statistically significant local pollen assemblage zones (Fig. 3, Table 3). These zones roughly corresponded to the boundaries of the lithostratigraphical units and are interrelated with the plant macrofossil data. The sediment accumulation rate (AR) was relatively constant, ranging between 0.16–0.8 cm^{-2} yr^{-1}; thus, the pollen sample resolution was, on average, 65 years.

Tree pollen that was considered exotic to the LG environment, such as termophilous taxa *Alnus*, *Corylus*, *Tilia*, *Quercus*, *Ulmus*, *Fraxinus*, and *Carpinus*, presumably inwashed from older deposits, was summarised as "redeposited pollen" (Fig. 3). Several of above mentioned pollen, but also some of the *Betula* pollen grains, which are usually considered to be locally produced, seemed corroded and

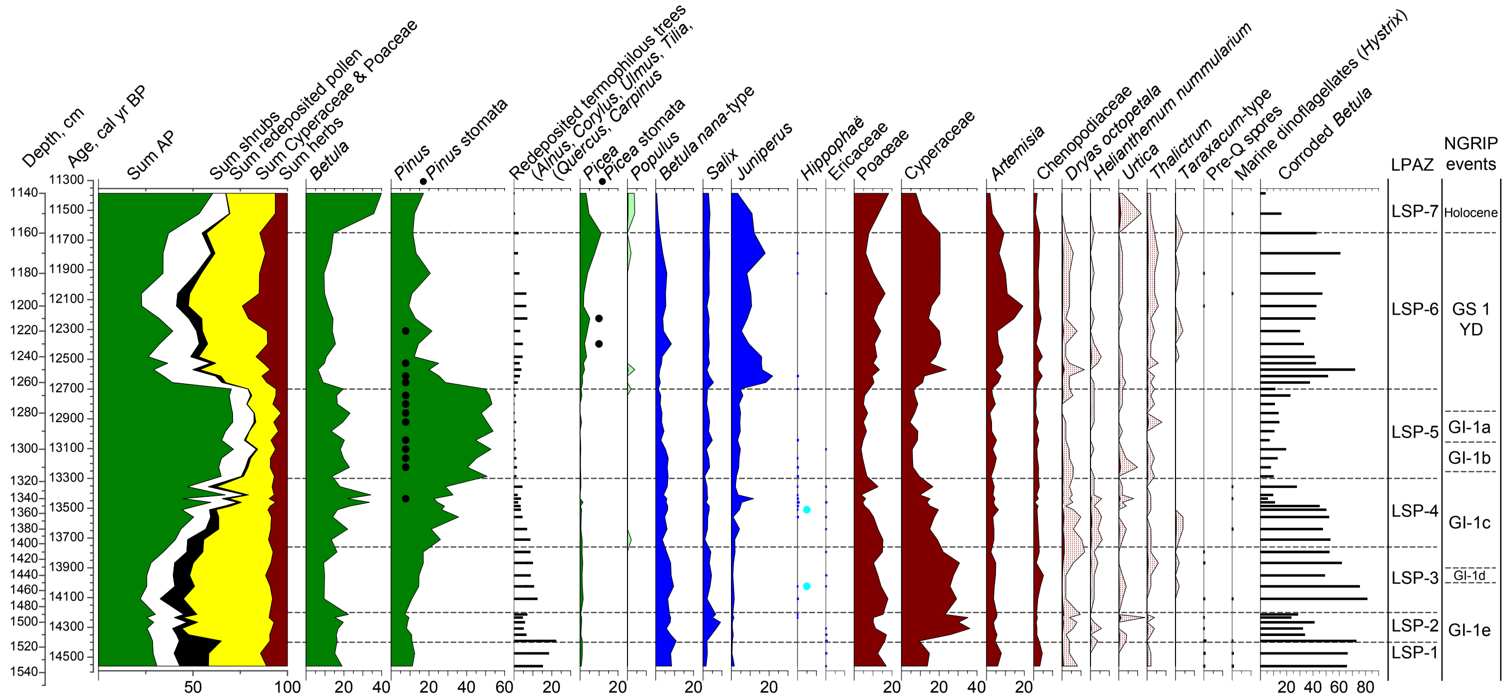

Figure 3. Percentages of selected pollen types (shading is an exaggeration at ×10) and other microfossils; statistically significant pollen assemblage zones (LPAZ) and NGRIP events for the pollen stratigraphy of the Lake Lielais Svētiņu sediment profile are shown.

Table 3. Lake Lielais Svētiņu statistically significant local pollen assemblage zones (LPAZ)

Depth, cm	Age, cal yr BP	LPAZ	LPAZ description	Vegetation type
1140–1160	11 650–11 390	LSP-7	AP dominates up to 60%, *Betula* reaches 40%, *Ulmus* and *Populus* appear, shrubs and NAP decline slightly. Corrosion is low. PAR of AP rises to Holocene levels.	Holocene, forest expansion
1160–1265	12 700–11 650	LSP-6	AP/NAP ratio is roughly 30/70, tree types *Betula* and *Pinus* are less than 20%, *Picea* is present as pollen and occasional stomata, of shrubs *Juniperus* culminates (20%). The NAP is dominated by Cyperaceae, Poaceae, *Artemisia*, Chenopodiaceae, *Dryas octopetala*, *Thalictrum* and *Helianthemum nummularium*. High relative abundance of corroded and in-washed pollen grains is observed. *Betula* and *Pinus* PARs are generally under 1000 grains cm^{-2} yr^{-1}.	Younger Dryas, open forest tundra with scattered birch, pine and spruce
1265–1315	13 300–12 700	LSP-5	AP dominates up to 70%, *Pinus* reaches over 50%, pine stomata are recorded, shrubs, NAP and redeposited pollen grains decrease. Green-algae flourish. *Betula* PAR stays around 4000 and *Pinus* PAR increase to an astonishing 14 000 grains cm^{-2} yr^{-1}.	Allerød warming, mixed pine-birch forest with a distinct dominance of pine
1315–1405	13 760–13 300	LSP-4	AP share gradually rises at the expense of NAP and around 13 600 cal yr BP surpasses it. *Pinus* and *Betula* PARs reach over 1000 grains cm^{-2} yr^{-1} 13 650 cal yr BP, *Betula* PAR peaks at 13 300 cal yr BP and stays around 4000 grains cm^{-2} yr^{-1}. All water plants and animals thrive since 13 400 cal yr BP.	Early-Allerød, developing birch-pine forest tundra
1405–1490	14 200–13 760	LSP-3	NAP dominates over AP (20%). The sum of redeposited termophilous trees is high. *Betula*/*Betula nana*-type relationship is in favour of the latter. *Hippophaë* appears. *Pinus* and *Betula* PARs stay under 500 grains cm^{-2} yr^{-1}.	The GI-1d (Older Dryas) cooling, treeless pioneer tundra
1490–1515	14 400–14 200	LSP-2	AP/NAP ratio is 40/60; tree types *Betula* and *Pinus* are less than 20%, shrubs *Betula nana* and *Salix* are present. The NAP part is dominated by Cyperaceae, Poaceae and *Dryas octopetala*. Low relative abundances of corroded and in-washed termophilous pollen grains. *Betula* PAR is just over 500 grains cm^{-2} yr^{-1}, *Salix* PAR reaches 300 grains cm^{-2} yr^{-1}. AR of green algae *Pediastrum* and *Tetraedron* are high.	The GI-1e (Bølling) warming, treeless herb/shrub tundra. Higher productivity in lake
1515–1535	14 560–14 400	LSP-1	NAP dominates over AP. The sum of redeposited termophilous trees is highest, over 20%. *Bryales* mosses which are present throughout the LG are missing in this zone. *Betula nana*-type peaks. Tree pollen PARs are below 500 grains cm^{-2} yr^{-1}.	Early-Bølling, treeless pioneer tundra, establishment of vegetation cover

degraded. Grains of more smooth-surfaced pollen types, such as *Betula*, *Alnus, Corylus* and *Carpinus*, but also *Tilia* and *Ulmus*, were attached corrosion estimates (corroded/not corroded) and later used as a measure of redeposition or inwash from older sediments. While the corrosion percentage of *Ulmus*, *Tilia* and *Carpinus* was always 100%, that of *Alnus* and *Corylus* varied between 75–100%. The percentage of redeposited pollen shows a reversed distribution in comparison with OM values, relative abundance of tree pollen types and tree pollen PAR (Fig. 4). The corrosion of birch pollen is clearly smaller in LPAZs LSP-2, LSP-5 and LSP-7. The goodness-of-fit (R^2) between the sum of redeposited pollen and the corroded *Betula* was 0.55. If an average value over three samples is used, the R^2 increases to 0.71 (Fig. 5), indicating a good correlation. The relationship between *Betula* tree-type pollen and *Betula nana*-type pollen (indicated as the deviation from the mean value) shows a good positive correlation with dwarf birch macrofossil finds (Fig. 6A), i.e., in periods in which dwarf birch macrofossils are present, the deviation is in favour of *Betula nana*-type pollen, and corroded birch pollen dominates. Deviation from the mean ratio of *Pinus* versus "one air-sacked *Pinus*" (P/osP) shows a highly negative deviation, i.e., more broken pine pollen in periods in which the pine PAR is low and there are no pine macrofossils (Fig. 6B). Interestingly, the ratio of P/osP in the LG deposits of Lake Udriku, North Estonia (Amon and Saarse, 2010), is always very low (unpublished data), which is indicated as an additional broken line in Fig. 6A. In general, the Holocene ratio of P/osP measured in several Estonian pollen datasets is comparable with the values of LS pine pollen in the period of 13 700–12 750 cal yr BP (Fig. 6), where we assume pine forest was present according to a high pine PAR and macrofossil evidence. The assumption that part of the birch and pine pollen is also redeposited

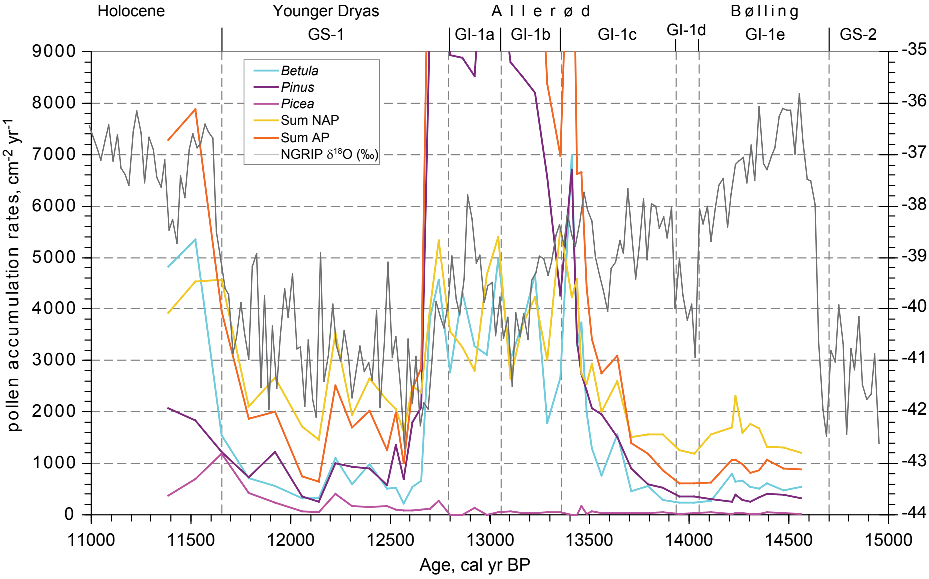

Figure 4. Pollen accumulation rates (PARs) of selected tree pollen types and the NAP total of the Lake Lielais Svētiņu sediment profile.

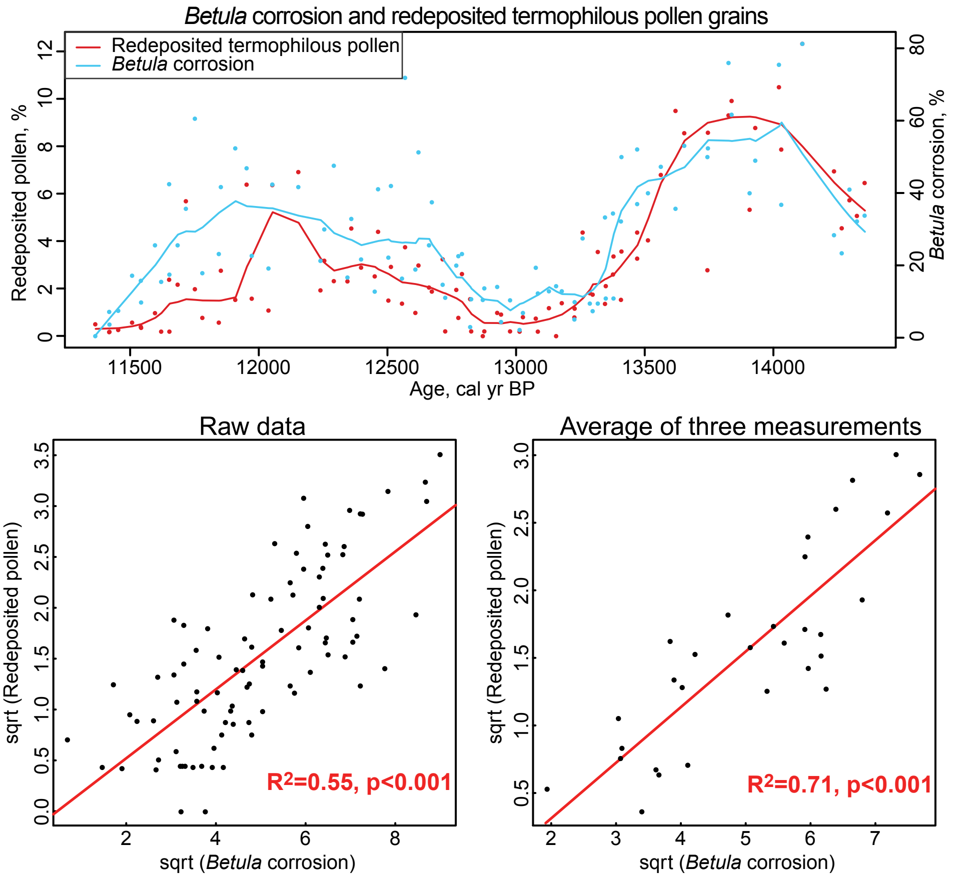

Figure 5. Corroded and degraded grains of *Betula* and redeposited termophilous pollen grains (*Alnus*, *Corylus*, *Carpinus*, *Quercus*, *Ulmus*, *Tilia* pollen types). The goodness-of-fit (R^2) between the abundance data for redeposited termophilous, i.e., inwashed pollen, and the corroded *Betula* pollen is 0.55 (R^2 for the three measurement average is 0.71).

in LG sediments, likewise the termophilous pollen grains, is obvious. The question is how much of that pollen is redeposited. We think that by using the degradation data of pine and birch pollen in combination with plant macrofossil evidence, we could subtract a certain portion of pollen grains from the record and give a more accurate picture for the LG vegetation.

4.3. Plant macrofossil evidence

The Lake LS LG sediment record was divided into 77 samples for plant macrofossil analysis, and in total, more than 31.5 l of sediment was examined for plant remains. A total of 30 vascular plant species, genus or families were identified. The concentration of plant macrofossils was multiplied by 100 to plot the results

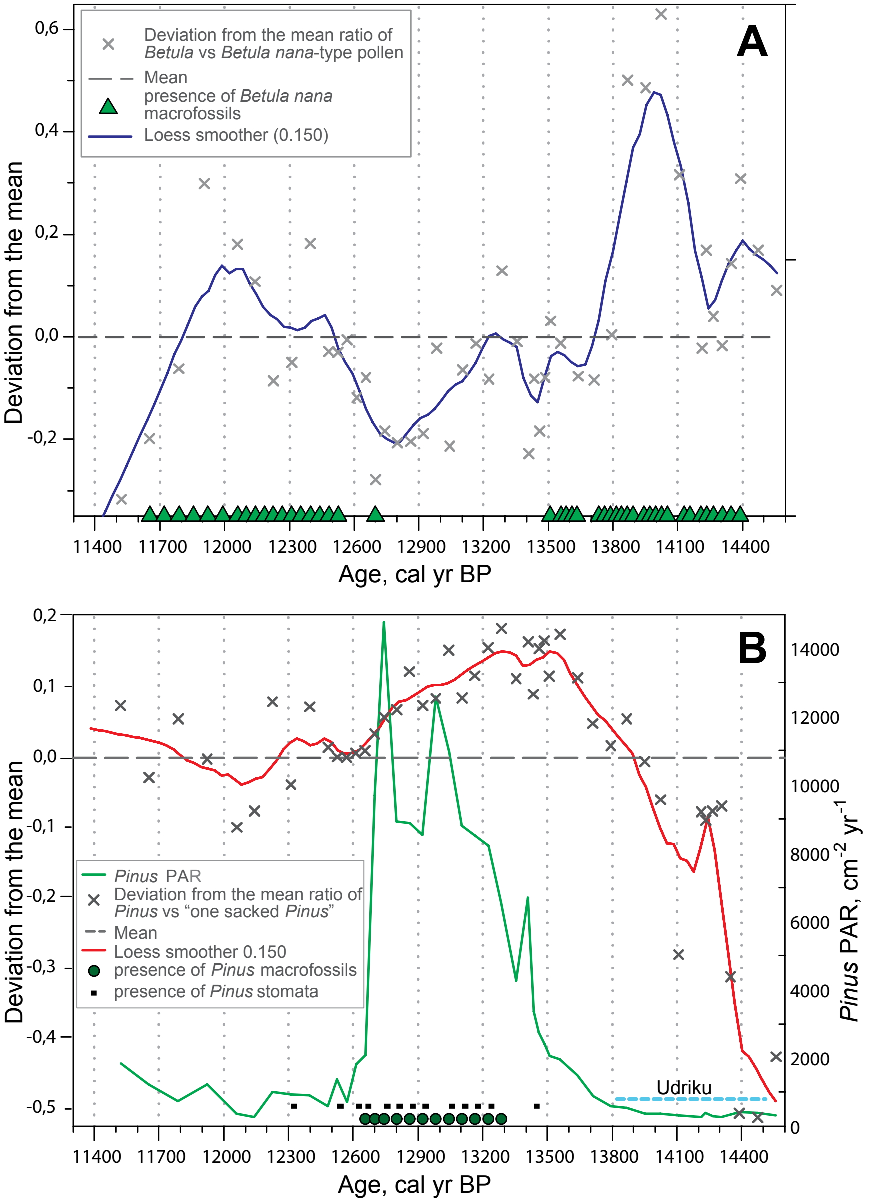

Figure 6. **A**. The relationship between *Betula* tree-type pollen and *Betula nana*-type pollen, indicated as deviation from the mean value in relation to dwarf birch macrofossil finds. When dwarf birch macrofossils are present, the deviation is in favour of *Betula nana*-type pollen, and corroded birch pollen dominates, as in Fig. 5. **B**. Deviation from the mean ratio of *Pinus* versus "one air-sacked *Pinus*" (P/osP); more broken pine pollen is present in periods in which the pine pollen accumulation rate is low and there are no pine macrofossils. The ratio of P/osP in the LG deposits of Lake Udriku, North Estonia (Amon and Saarse, 2010), where tundra conditions prevailed over the whole LG period, is constantly very low (unpublished data), indicated as a broken blue line.

Table 4. Lake Lielais Svētiņu plant macrofossil assemblage zones

Depth, cm	Age, cal yr BP	Zone	Zone description	Vegetation type
1140–1160	11 650–11 390	LSM-7	Zone is based on two samples that contain remains of conifer (*Picea*) and deciduous trees (tree birch, aspen), no shrub macrofossils were recorded. Grasses (*Typha*) and *Juncus* are present.	Mixed forest expansion
1160–1265	12 700–11 650	LSM-6	Pine and deciduous tree (tree birch, aspen) macrofossil abundance drops quickly and vanishes in the start of the zone. In the lower part of the zone, the amount of plant macrofossils is low. In upper part of zone, spruce (*Picea*) macrofossils appear, dwarf birch and *Dryas* remains re-appear in the same layers. Telmatic (*Juncus, Carex*), aquatic (*Potamogeton, Hippuris, Batrachium*) and grasses are present.	Treeless open landscape to mixed tundra forest
1265–1315	13 300–12 700	LSM-5	The assemblage changes quickly from birch forest to mixed conifer forest, dominant tree species are pine (*Pinus*) and tree birch (*Betula*). *Populus tremula* is present. The number and species composition of aquatic species is stable (*Potamogeton, Zannichellia, Hippuris*). Telmatic plants, herbs and grasses are present (*Juncus, Carex,* grasses, *Saxifraga* etc.).	Mixed conifer forest
1315–1405 1315–1350	13 500–13 300	LSM-4a,b	*B.nana* disappears abruptly in favour of tree birch (*Betula* sect *Albae*). Telmatic plant remains are found in every sample. Herbs (*Saxifraga*, *Alchemilla*, Poaceae) and grasses are present.	Birch forest
1350–1405	13 760–13 500		The majority of macrofossils of this subzone are *B.nana* leaves; *Dryas* is present in one sample. Few grasses and telmatic plant remains are found.	Tundra
1405–1490	14 200–13 760	LSM-3	The number of plant macrofossil declines. The amount of shrub and *Carex* remains decreases. *Dryas octopetala* and *Betula nana* remains are present in most samples although in small numbers. Telmatic plants (*Selaginella, Carex, Juncus*) are present. The first appearance of Poaceae and *Saxifraga* plant macrofossils.	Shrub herbaceous tundra
1490–1515	14 400–14 200	LSM-2	Zone is characterised by remarkable rise in amount of plant macrofossils. Characteristic is abundance of *Betula nana* remains (leaves, seeds). Other shrubs present are *Salix polaris* and small quantity of *Dryas octopetala*. Wooden material is frequently found in samples. Telmatic plants are numerous (*Carex, Juncus*), *Potamogeton* spp. is present.	Shrub wetland tundra
1515–1530	14 500–14 400	LSM-1	The samples contain no or very few plant remains (*Carex* seeds).	Pioneer community

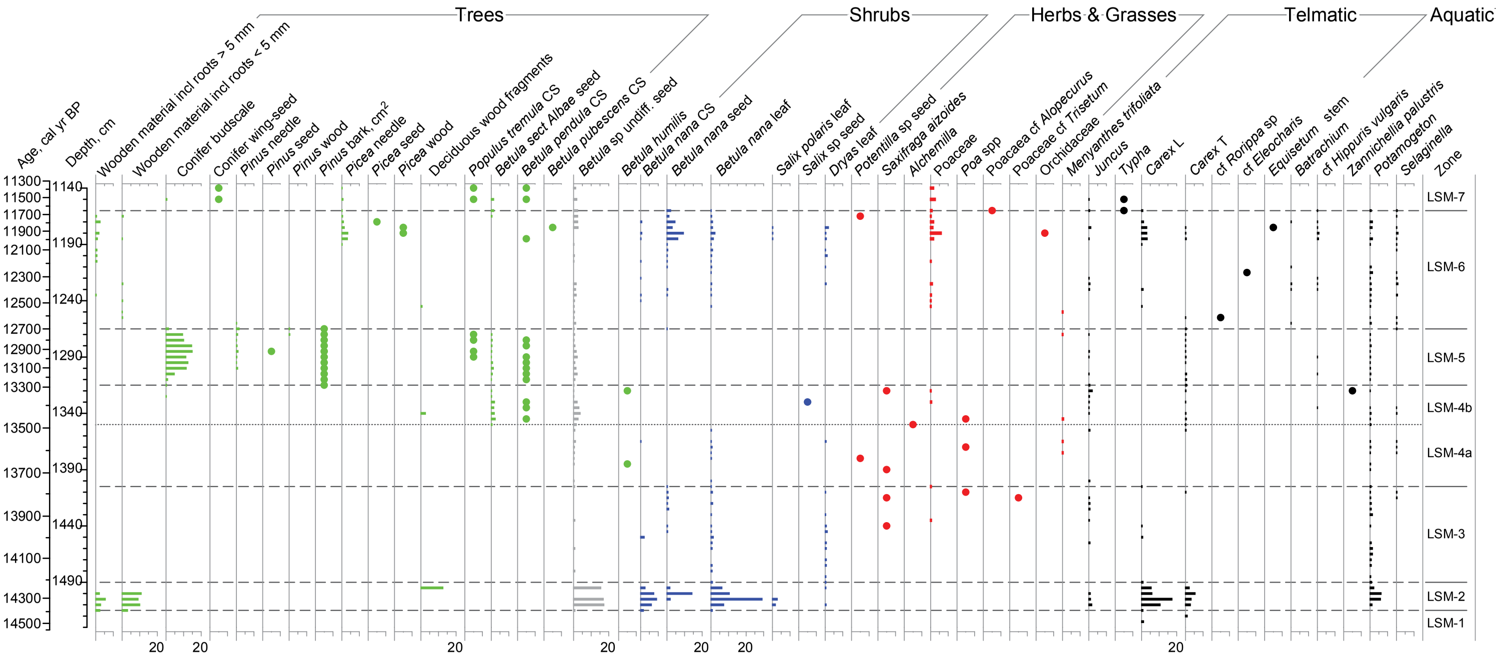

Figure 7. The concentration of plant macrofossil and limnic animal remains per 100 cm^3 of sediment from the Lake Lielais Svētiņu sediment profile.

on a diagram (Table 4, Fig. 7), therefore presenting the number of macrofossils in 100 cm^3.

4.4. Microscopic limnic evidence

Most of the sediment sequence was devoid of diatoms; however, an abundant diatom assemblage was ascertained between the period of 13 300 and 13 000 cal yr BP. Altogether, 76 diatom taxa belonging to 27 genera were encountered. The taxa that occur at a high relative frequency include epipsammic, small-sized fragilarioid diatoms, such as *Fragilaria brevistriata*, *F. construens*, *F. construens* var. *venter* and *F. lapponica*, as well as epipelic *Amphora pediculus*, *Campylodiscus noricus* and *Gyrosigma attenuatum*. Planktonic diatoms are relatively rare (1–3%). Although the diatom composition does not show considerable changes, the diatom concentration has sudden and short-lived peaks at 13 200 and 13 000 cal yr BP, which is synchronous with the curve of green algae accumulation rate (AR, Fig. 8). The ARs of green algae (*Pediastrum*, *Tetraedron*, *Scenedesmus* and *Botryococcus*) as well as Cladocera are high at intervals spanning 14 400–14 200 and 13 300–12 700 cal yr BP and in the Holocene.

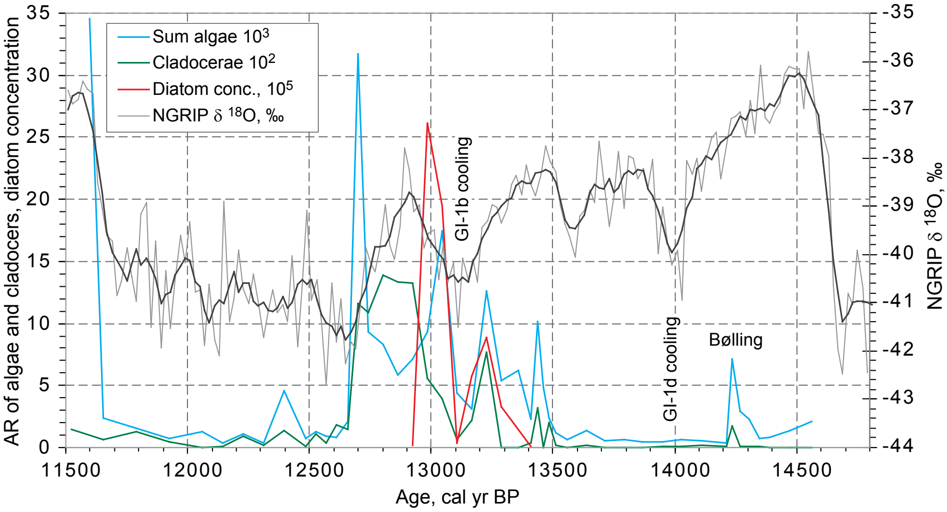

Figure 8. Accumulation rates (AR) of green algae and cladocera as well as diatom concentration in the Lake Lielais Svētiņu sediment profile.

5. Discussion

5.1. Deglaciation of eastern Baltic area and associated pioneer vegetation communities

Lake LS is situated in the East Latvian glacial lowland (Zelčs and Markots, 2004) between the Vidzeme and Latgale glacial uplands. The area was shaped and influenced by the Lubana glacier system, which was part of a larger ice stream complex that extended to Western European Russia and Lake Ladoga, and it entered the Lubana basin from the northeast (F^1 ice stream in Kalm, 2010). The dynamics of ice lobes were largely controlled by bedrock and pre-LGM topography (Zelčs and Markots, 2004), climate and connection with source areas. Geomorphologically, Lake LS and the East Latvian lowland are situated between the Middle and North Lithuanian (Haanja) Moraine (Rinterknecht et al., 2006) and consequently, based on ^{14}C and ^{10}Be dates from these ice marginal formations, they date approximately to 13 500±1000 ^{14}C yr BP (~13 500 ^{10}Be yr BP) and 13 300±1100 ^{14}C yr BP (~13 300 ^{10}Be yr BP), respectively (Rinterknecht et al., 2008). In calibrated years (OxCal 4.1, Intcal09), the median ages of the abovementioned ^{14}C ages and thus also the glacier retreat from the East Latvian lowland would be approximately 16 300–16 000 cal yr BP. Zelčs and Markots (2004) estimate the age of the North Lithuanian Moraine (Linkuva, Haanja) as approximately 13 200 ^{14}C yr BP (calibrated median ca 16 000 cal yr BP). Kalm (2006) proposed the age of the Haanja Moraine to be 15 700–14 700 cal yr BP, later pinpointing it to approximately 15 000 cal yr BP (Kalm et al., 2011). Thus far, the radiocarbon age estimations tend to be too old compared with those of Kalm et al. (2011), possibly because of the Raunis section in northern Latvia. The ^{10}Be ages seem to be rather young; the possible problem with ^{10}Be ages is that we do not know when the rock surfaces of the glacial erratic boulders that were dated melted out of the glacier, whether it was soon after the glacier retreated or when the erratic boulders were hidden in dead ice fields for ages.

The interpreted deglaciation processes based on age estimations of ice marginal formations suggest a rather slow ice retreatment rate. A large Lubana ice-dammed lake with a maximum water level altitude of 108 m a.s.l. (Zelčs and Markots, 2004) flooded the area afterwards, and Lake LS might have been in its southeastern part. The establishment of virgin terrestrial ice-free ground and the development of vegetation in the surroundings of Lake LS in eastern Latvia occurred at 14 560 cal yr BP, as derived from the age model (zones LSP-1 and LSM-1; Figs 3, 7), in the relatively warm climatic oscillation of the LG, which is termed GI-1e (*sensu* Lowe et al., 2008). By that time, the environmental conditions were suitable to support pioneer vegetation. Pollen and plant macrofossil analysis results suggest that the pioneer communities around Lubana basin in the glacial foreland were rather scarce: only two seeds of *Carex* were found, and the pollen spectra contain numerous pollen grains of redeposited termophilous trees (*Alnus*, *Corylus*, *Carpinus*, *Quercus*, *Ulmus* and *Tilia*, in total 20%), of which large amounts (over 70%) were also corroded. Marine dinoflagellates (*Hystrix*) and pre-Quaternary spores are common, suggesting the reworking of older material. A similar reworking of pollen in the early LG sediments had already been noted by Iversen (1954) at the classic Bølling Sø site in Denmark. The pine and birch pollen PARs are below 500 grains cm^{-2} yr^{-1}, and the birch pollen corrosion index is above 70%, suggesting, rather, that they were not present in the vegetation. The *Betula nana*-type pollen percentages are the highest in this pioneer phase, and the deviation from the mean ratio of dwarf birch versus birch pollen (Fig. 6A) indicates positive anomalies, although *Betula nana* macrofossils appear only at 14 400 cal yr BP, i.e., approximately 100 years after the deglaciation. Highly negative anomalies occur in the deviation from the mean pine degradation, pointing also to high pollen resedimentation and not to the local production of any tree pollen. If we subtract the supposedly resedimented portion of pine and birch pollen according to pine pollen degradation (P/osP = 75 %) and birch pollen corrosion (mean = 68.3%) from the total record, we end at PAR below 100 grains cm^{-2} yr^{-1} for pine and 200 grains cm^{-2} yr^{-1} for birch, which are far below the limit of presence for these taxa in present conditions (Hicks, 2001).

However, the favourable climatic conditions during phase GI-1e (in older scientific literature, the described first postglacial stable community is often named “Bølling”) allowed the pioneer community to be replaced by a stable and more species-rich vegetation type in ~100 years (LSP-2 and LSM-2). Most likely, a treeless tundra community consisting of shrubs (*Betula nana, Dryas octopetala, Salix polaris*) and telmatic plants (*Carex, Juncus*) spread between 14 400 and 14 200 cal yr BP, as there is no macrofossil evidence of tree birch. The *Betula* sp. undiff. seed curve (Fig. 7) in this time interval should be regarded as *B. nana*; although later, in Allerød, the same curve most likely indicates tree birch. To date, tree birch evidence from the Bølling period is also lacking in Denmark (Mortensen et al., 2011). The amount of plant macrofossils from this sediment interval is surprisingly high, hinting at a rather productive community supported by suitable climatic and environmental conditions. Another reason might be the extreme openness of the landscape that favoured fast transportation of plant remains into the lake and, therefore, good preservation in the sediment record. A third assumption regarding the richness of plant macrofossils may point to the origin of Lake LS; namely, the OM rich Bølling strata may be formed *in situ* on top of the degrading ice field when material melting out of the glacier ice forms a wet soil cover on top of the ice. This scenario is contradicted, however, by a number of aquatic species, both algae and cladocera, that indicate lacustrine conditions.

Although the macrofossil data suggest treeless conditions during GI-1e, the pollen evidence points to several arguments that might explain the opposite. First, the uncorrected PAR of birch reaches over 500 and up to 800 grains cm^{-2} yr^{-1} by the end of the warm period at 14 200 cal yr BP; second, the corrosion index of *Betula* drops drastically between 14 400 and 14 200 cal yr BP, which might indicate that at least some portion of the birch pollen rain was locally produced, or at least we cannot rule out the idea. Applying the degradation/corrosion index for this period, the PARs for pine and birch are below 200 and 500 grains cm^{-2} yr^{-1}, respectively; for the latter, this is value close to the presence limit, but not enough to detect macrofossils. Paus (1995) argues that birch PAR values as low as 200 grains cm^{-2} yr^{-1} indicate the local presence of tree birch during the Bølling in south Norway, yet without macrofossil evidence. Currently, we remain doubtful about the presence of tree birch in Bølling in the eastern Baltic area. Approximately 14 200–14 000 cal yr BP pollen grains and other microfossils (hair) of *Hippophaë* show some climate amelioration, as *Hippophaë* occurrences seem to precede the truly warmer periods of the LG and the Holocene. *Hippophaë* was also an important indicator of open landscape for Iversen (1947). Otherwise, the pollen and macrofossil data agree on shrub–herb tundra conditions, as pollen evidence also points to an elevated signal of *Salix*, Ericaceae and herbs. An early dominance of *Salix polaris* and *Dryas* has also been noted at other sites in the Nordic countries (Bennike et al., 2004b; Karlsen, 2009; Paus, 1995).

The aquatic life quickly responded to climatic amelioration (Fig. 8). The ARs of green algae *Pediastrum* and *Tetraedron* and Cladocerans are high, and the total AR reached 7000 coenobia cm^{-2} yr^{-1}.

A comparable site, Lake Kurjanovas (Heikkilä et al., 2009), situated in the Mudava lowland area adjacent to Latgale upland from the east (Fig. 1), suggests that the deglaciation there was more than 16 000 cal yr BP, which is in accordance with the estimated ages of the nearby ice marginal zone (Rinterknecht et al., 2006). The Latgale upland (highest point 289 m a.s.l.) was a spreading area for two glacial complexes, F^1 and F^2 (Kalm, 2010). The area around Lake Kurjanovas within a different ice stream might have deglaciated earlier than the surroundings of Lake LS. Lake Kurjanovas is situated somewhat higher than Lake LS (111 m.a.s.l. and 96 m.a.s.l., respectively), which probably promoted earlier deglaciation and terrestrialisation. However, the time-scale of Lake Kurjanovas is rather tentatively extrapolated, and authors suggest handling the chronology for the lower part of the sediment with caution. It is likely that the start of vegetation development and its preservation in the lake sediments east of the Latgale upland took place earlier than in the eastern Latvian glacial lowland northwest of the Latgale upland.

Comparing the vegetation development, a treeless wetland shrub-tundra (*B. nana*) community prevailed in the Lubana glacial lowland, while *Dryas* tundra with possible scarce tree birches existed east of the Latgale upland, around Lake Kurjanovas (Heikkilä et al., 2009).

5.2. The GI-1d cooling and vegetation recovery thereafter (14 200–13 300 cal yr BP)

The GI-1d, or "Older Dryas" in early Baltic literature, was a short cooling episode. This period, centred at 13 950 cal yr BP, is ca 125 years in the Greenland ice data (Lowe et al., 2008), before the GI-1c warmer climatic episode. The cold climate interval is also well reflected in the palaeobotanical record of Lake LS.

The total concentration of plant macrofossils declines sharply at 14 200 cal yr BP. The species composition found at 14 200–13 300 cal yr BP (plant macrofossil zones LSM-3 and the LSM-4a subzone) does not change much compared with the GI-1e warm period and still indicates a sparse treeless *B. nana–Dryas* tundra community, but in much lower concentrations and without woody material. The soil was dryer than in the previous time interval, and the number of telmatic remains is modest. Instead, grasses and *Saxifraga aizoides* appeared. The latter species prefers dry, stony and barren soils as a growing environment. Since 13 760 cal yr BP (in the LSM-4a subzone), the soil again became more favourable to telmatic species (*Menyanthes*), and *S. aizoides* disappeared. The pollen record of the post-Bølling cooling displays very low (under 300 grains cm^{-2} yr^{-1}) PARs for birch and pine for a period of 14 100–13 800 cal yr BP, i.e., for a longer period than the actual cooling that took place in the Greenland ice core data (Lowe et al., 2008). The pollen corrosion is high (*Betula* 62%, total corrosion 70%), and the deviation from the mean ratio of dwarf birch versus birch pollen shows the highest positive anomalies, suggesting *B. nana* dominance in the local pollen rain (Fig. 6A). The corrected tree birch-type PARs for the GI-1d cooling in general are comparable to the earliest stages of the pioneer vegetation – below 200 grains cm^{-2} yr^{-1}. Before 13 800 cal yr BP, the deviation from the mean pine degradation is negative, pointing to the non-local origin of *Pinus* pollen during GI-1d (Fig. 6B). The corrected *Pinus* PAR at approximately 350 grains cm^{-2} yr^{-1}, however, is higher than in previous periods and indicates a constant rise throughout the earlier part of the LG, thus suggesting an ever increasing pine pollen source in the south. Tree pollen (pine and birch) percentages and PARs gradually rise and at approximately 13 800 yr BP (the onset of the warmer GI-1c event), surpass the 500 grains cm^{-2} yr^{-1} limit (local presence sensu Hicks, 2001; Seppä and Hicks, 2006) and at 13 650 cal yr BP, surpass the 1000 grains cm^{-2} yr^{-1} (birch forest) limit. First, macrofossils of the tree/shrub birch *Betula humilis* appear at 13 680 cal yr BP, so the early open "birch forest" in reality might have been one-metre-high brushwood of dwarf and shrub birch. Approximately 200 years later, at 13 460 cal yr BP, *B. nana* suddenly disappears from the plant macrofossil record. At the same level, a tree birch section with *Betula* sect. *Albae* and *Betula pubescens* is introduced, marking the start of a true tree birch forest in the area (Fig. 9). In Denmark, tree birch arrived earlier, at 13 600 cal yr BP, but pine did not arrive there until the Preboreal (Mortensen et al., 2011). At the same time, the PARs of *Pinus* and *Betula* reach over 2000 grains

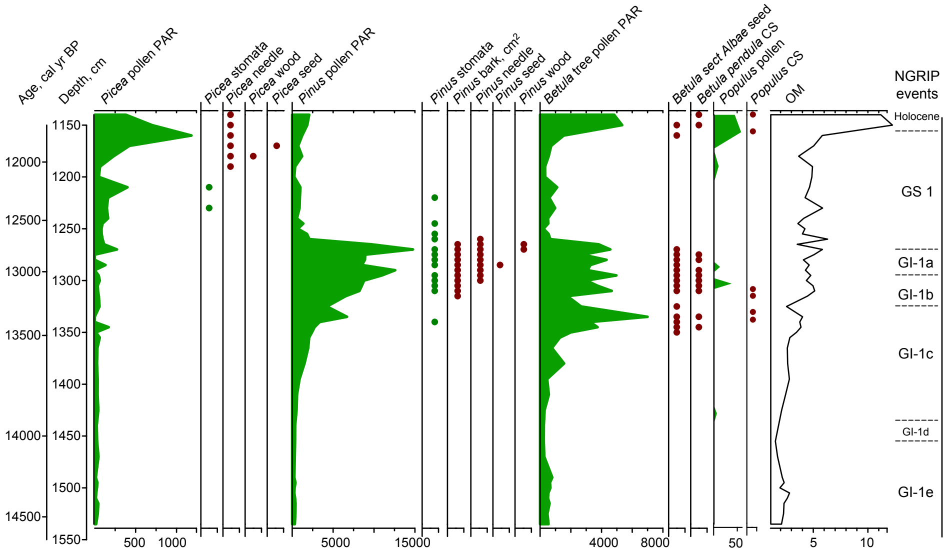

Figure 9. Summary macrofossil and microfossil evidence of tree types in the Lake Lielais Svētiņu sediment profile.

cm^{-2} yr^{-1}, and the *Betula* PARs reach a level of 4000 grains cm^{-2} yr^{-1} at 13 300 yr BP, remaining there until the Younger Dryas. Also, the corrosion percentages of birch pollen drop to 10%, indicating that most of the birch pollen was locally produced. The occurrence of numerous tree birch macroremains and high PARs confirm the presence of (tree) birch forests in eastern central Latvia, in the Lubana basin around Lake LS. Moist and telmatic conditions prevail around the lake, as macrofossils of *Juncus, Carex* and *Selaginella* are present as well as Bryales, *Sphagnum*, *Equisetum* and *Botrychium* spores and *Drepanocladus* leaf fragments in the pollen and spore record.

5.3. The Late-Glacial forest at 13 300–12 700 cal yr BP (GI-1b and GI-1a)

The composition of plant macrofossils in zone LSM-5 (13 300–12 700 cal yr BP) demonstrates the effective introduction of *Pinus* and the formation of a mixed conifer forest. The presence of *Pinus* and pine forest is confirmed by a variety of macrofossils: bark, wood, needles, seeds. Since the find of an unidentified conifer budscale at 13 400 cal yr BP, pine bark was identified since 13 300 cal yr BP and pine needles since 13 100 cal yr BP (Fig. 9). From the pollen signal, pine stomata are found prior to macrofossils, namely at 13 450 cal yr BP. The first pine stomata finds are associated with a *Pinus* PAR over 3000 and the pine macrofossil finds with a *Pinus* PAR over 4000 grains cm^{-2} yr^{-1}. The maximum pine PAR reaches far beyond 10 000 (14 000 max) grains cm^{-2} yr^{-1} in the late Allerød, just before the Younger Dryas cold spell starts. Such high pine PARs seem surprising

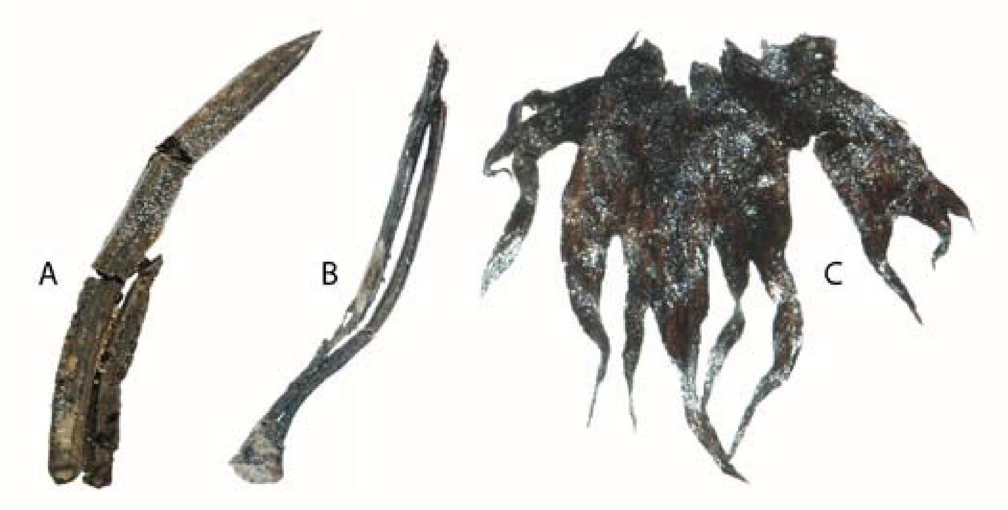

Figure 4. Photos of A. *Picea* needle (7x), B. *Pinus* needle (6x) and C. *Populus tremula* catkin scale (18x) from the Lake Lielais Svētiņu sediment profile at downcore sample depths of 1185, 1270 and 1290 cm, corresponding to ages of ca 12 000, 12 750 and 13 000 cal y BP.

because just 140 km to the north, around Lake Nakri in southern Estonia, pine PARs seldom exceed 2000 grains cm^{-2} yr^{-1} levels (Amon et al., 2011), and to date, no pine macrofossils are found north of LS in the eastern Baltic or, for instance, in Denmark, which is at an equal latitude with Latvia (Bennike et al., 2004a). In addition to *Pinus*, deciduous trees formed a part of the forest community, namely birch (*Betula pendula*) and aspen (*Populus tremula*). The find *Populus tremula* catkin scales (Fig. 10) at 13 000–12 750 cal yr BP, during the warmest period of the GI-1a (Allerød) warming, makes it one of the few records of this plant species macrofossils in the LG period in Eurasia (Binney et al., 2009). Occasional pollen finds of *Populus* in the LG sediments of Lake LS do not coincide with the macrofossil data until the start of the Holocene. During GI-1a, the pollen grains of *Populus* are not found, probably due to the poor preservation of thin-walled pollen grains. In most of the cases, pollen seems to precede the macrofossil signal. Birch in the Allerød pine forest of eastern Latvia seems suppressed, with its PAR values of approximately 4000 grains cm^{-2} yr^{-1} during GI-1a. In south Estonia, birch is the only dominant tree, with recorded macrofossils and PARs over 4000 grains cm^{-2} yr^{-1} (Amon et al., 2011). The deviation of the *Betula*/*Betula nana*-type from the mean ratio (Fig. 6A) indicates negative anomalies, and *Betula nana* macrofossils are missing from the record from 13 500 to 12 750 cal yr BP, indicating that tree birch was probably the main pollen producer.

At the local macrofossil scale, the growing conditions favour telmatic plants (*Juncus, Carex, Menyanthes*) instead of grasses and herbs (no species found in this interval), which indicates that during the Allerød warm period, forest surrounded the lake from all sides and that the telmatic record comes from a narrow strip just around the lake shore. The void of NAP macrofossils is supported by low percentages of herbs in the pollen signal, though the PAR of NAP is high, indicating that pollen production in the warm period was favourable.

The GI-1a warm period was also beneficial for aquatic life, which responded to the climatic amelioration. The AR of green algae *Pediastrum*, *Tetraedron*, *Botryococcus* and *Scenedesmus* rises rapidly after 13 500 cal yr BP, and the algae thrive until 12 700 cal yr BP. The same can be said about Cladocerans. In addition, a rather rich diatom flora was developed between 13 300–13 000 cal yr BP. In fact, this is the first time when diatoms are recorded in Estonian and Latvian LG sediments, and their evidence is used for palaeoenvironmental reconstructions. The infrequent occurrence of planktonic diatoms in the assemblage indicates a comparatively shallow limnic environment. Alternatively, the rarity of planktonic diatom species suggests rather cold winters, prolonged duration of the ice cover and a shorter growing season, which hampered the development of the phytoplankton community in the deeper water environment. The GI-1b (Gerzensee) cold event centred on 13 150 cal yr BP is recognised in the aquatic signal, but not in the terrestrial (pollen nor macrofossils). In Swiss lakes, the GI-1b oscillation occurs during a pine-dominated phase as well, and some authors (Lotter et al., 1992) argue that its vegetation effect cannot be determined palynologically. However, Wick (2000), based partly on the same material, shows a significant correlation between $\delta^{18}O$ and pollen for the Gerzensee oscillation. The 200-year cold period is reflected as a remarkable decrease in the AR of Cladoceran remains, the AR of algae (especially *Pediastrum* and *Scenedesmus*) and the diatom concentration in LS material. The life cycle of aquatic organisms in arctic lakes is dependent on climate related variables, such as the duration and extent of ice cover (Douglas and Smol, 1999). During the colder and longer winters at approximately 13 150 cal yr BP, a thick ice cover probably formed, which delayed the break-up of lake ice in the deeper areas, and only narrow areas in the littoral zone were ice-free. The intra-Allerød/Gerzensee cold period GI-1b was detected as reduced cladoceran concentrations in Bølling Sø (Bennike et al., 2004b; Sarmaja-Korjonen et al., 2006) and is well represented in the drop of tree pollen PARs in Lake Nakri, southern Estonia (Amon et al., 2011). One might argue that sites more northern and proximal to the ice edge, such as Nakri, are more sensitive for recording terrestrial vegetational shifts compared with fully established pine forests in central Latvia.

Heikkilä et al. (2009) found similar mixed conifer forests around Lake Kurjanovas in the 'Bølling/Allerød' interval. In their study, the mixed forest period started several hundred years earlier, ca 14 400–14 000 cal yr BP, when treeless tundra prevailed that developed into birch forest in areas around Lake LS in eastern Latvia. The earlier arrival of pine and the formation of dense forest in the Kurjanovas area may be tied to its south-easterly location. Lake LS is situated northeastwards from Lake Kurjanovas, i.e., to the direction of the deglaciation; the area in the southeast deglaciated earlier, and the state of environmental conditions was more developed and suitable for new species to migrate. The narrow transition zone from tundra to boreal forest might have been located between the Latgale upland and the eastern Latvian lowland by ca 14 000 (14 400) cal yr BP. The transition zone moved north-westwards, reaching the eastern Latvian lowland at ca 13 450 cal yr BP according to finds of pine stomata in Lake LS. Pine migrated further and perhaps had a sparse colony in southern Estonia at ca 13 300 cal yr BP (stomata evidence, Amon et al., 2011). However, the migration there stopped because at 13 200 cal yr BP, the ice front was still at the Palivere ice marginal zone in north Estonia (Saarse et al., in prep), and treeless tundra conditions prevailed in northern Estonia until the Holocene warming (Amon and Saarse, 2010).

The surroundings of Lake Kurjanovas have a higher elevation compared with Lake LS, which might lead to drier soils that would be more suitable for pines compared with glacial lowland clayey soils. The 'Bølling/Allerød' interval of Lake Kurjanovas has been reported as a rather moist phase (Heikkilä et al., 2009), but the Lake LS sediments contain a variety of telmatic plant macrofossils from this period, except for a slightly drier interval at 13 900–13 600 cal yr BP. As an elevated area next to the upland, it was perhaps also better at trapping seeds from pine source areas southwards or southeastwards or even from the Latgale upland. In southeastern Lithuania, pine was also present at more than 14 000 cal yr BP (Stančikaitė et al., 2008) and in Belarus at the Allerød/Younger Dryas boundary (Makhnach et al., 2004).

A local sedimentological event took place inside the warmest part of the Allerød. The sediment composition changes in Lake LS at core depths of 1317–1332 cm (ca 13 300– 13 200 cal yr BP), when a distinctly laminated (varved?) clay interval formed consisting of ~20 varve couplets. Magnetic susceptibility increased, and organic matter content dropped remarkably. We can exclude the active glacier, which at that time was already in northern Estonia and was associated with the formation of laminated or varved clays with increased and rhythmical mineral matter input, most likely from the melting of dead ice on the Latgale upland through discharge channels on its slope (Zelčs and Markots, 2004).

5.4. GS-1 Younger Dryas cold event

The last and most prominent 1000 year cooling event before the start of the Holocene warming, the GS-1 (Lowe et al., 2008), remarkably affected the floral composition in the Northern Hemisphere, including eastern Latvia. Around Lake LS, the forest species declined abruptly from a maximal PAR at 12 700 to a PAR below 1000 grains cm^{-2} yr^{-1} at 12 600 cal yr BP, i.e., the response time for the pine forest to collapse was 100 years according to pollen accumulation data. Pine macrofossils disappear simultaneously with the pollen signal at 12 600 cal yr BP, yet occasional *Pinus* stomata are recorded throughout the GS-1. Aspen and birch plant macrofossils fade away earlier at 12 750 cal yr BP. The decline of birch PARs is more rapid compared with that of pine, which might explain the earlier disappearance of birch macrofossils. The landscape was altered to treeless shrub tundra once again. *Dryas octopetala, Salix polaris* and *B. nana* are present in the macrofossil record accompanied with high percentages of *Juniperus* (20%), Poaceae, Cyperaceae and *Artemisia*. The NAP ratio compared with AP is positive from 12 600–11 650 cal yr BP, yet the landscape is not entirely treeless, as pine and birch PARs drop below 500 grains cm^{-2} yr^{-1} only for short periods at 12 600–12 500 and 12 200–11 900 cal yr BP. The time between these extreme cold spells (12 500–12 200 cal yr BP) is illustrated as rather suitable for organic sedimentation, with up to 8% of OM, i.e., LG maximal values occur. In that warmer window inside the cold Younger Dryas, *Picea* is introduced in the region and is represented by stomata (12 400–12 200 cal yr BP), needles, seeds and wood (since 12 050 cal yr BP up to the Holocene) (Figs 9, 10). *Picea* PAR surpasses the 100 grains cm^{-2} yr^{-1} limit, which is the threshold PAR for the presence of spruce forest (Hicks, 2001), at already 12 750 cal yr BP, but only when the PAR occasionally exceeds 400 grains cm^{-2} yr^{-1} do the spruce macrofossils and the pollen signal coincide. The LG presence of *Picea* in Latvia has been demonstrated by other studies (Heikkilä et al., 2009; Koff and Terasmaa, 2011). However, in these studies, the spruce was introduced slightly earlier, at 12 900 cal yr BP, according to pollen signals, and at 12 400 cal yr BP based on macrofossil evidence (Heikkilä et al., 2009). The easterly glacial refugium of spruce has been shown in numerous publications (Saarse et al., 1999; Giesecke and Bennett, 2004), and it is not surprising that spruce migrated to the eastern Baltic so early. By this time, the environmental conditions and climatic factors important for vegetation development that were connected with the ice retreat pattern had been stabilised and were more or less equal over mid-Latvia – the ice front was already in southern Finland. Therefore, more local and climatic factors that inhibited or favoured the migration of *Picea*, such as elevation (Lake Kuži 191.5 m a.s.l.), soil development, moisture regime, might have been more important. Again, the more easterly location of Lake Kurjanovas might have favoured earlier and stronger spruce invasion (Giesecke and Bennett, 2004). However, the occurrence of spruce during the LG is limited to mid- or eastern Latvia: in northern Latvia (Lake Burtinieks), *Picea* is absent in GS-1 (Ozola et al., 2010) as well as in Estonia (Saarse et al., 1999; Amon et al., 2010, 2011). The combination of fossil pollen and genetic data of *Picea abies* reveals the LG maximum refugium area in the Russian Plain that became the basis of the so-called northern lineage of present spruce in Northern Europe (Tollefsrud et al., 2008; Giesecke and Bennett, 2004). The proposed area inhabited by the northern lineage of spruce in 10 000 cal yr BP extends from western European Russia to easternmost Latvia and the northernmost corner of Belarus, and it concentrically inhabits other areas.

5.5. Holocene warming and subsequent vegetation change

The Pleistocene/Holocene boundary at 11 650 cal yr BP is marked by changes both in vegetation composition and sediment type. The organic-rich gyttja accumulated instead of silts and clays, and the start of the Holocene warm period permitted forest reexpansion in the surroundings of Lake LS. Plant macrofossil data confirm the presence of mixed conifer forest (spruce, tree birch, aspen). *Betula nana* disappears both from the pollen and macrofossil records, and typical early Preboreal open birch forest with spruce, junipers and willows develop.

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